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The Zoogeography and Systematics of the Argentine Andean and Patagonian Pierid Fauna

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Abstract. The geographic distributions and systematics of the Pieridae of the Andean highlands and Patagonia, Argentine Republic, are reviewed. Previously unpublished records based on twelve years' field work by the author and collections in Argentina, the United States, the United Kingdom, etc. are provided to clarify zoogeographic and systematic problems in this fauna. *Tatochila blanchardii* is reduced to a subspecies of *T. autodice*. The taxa *T. arctodice*, *macrodice*, *sterodice*, *vanvolxemii* and *fueguensis* all become subspecies of the widespread polytypic species *T. mercedis*. The possibility that *Hypsochila wagenknechti* and *H. galactodice* are conspecific is discussed. Records of putative *galactodice* from the *puna* of Jujuy are presented. The taxonomic history of *Phulia nymphula* in Argentina is clarified, and its range extended south to western Neuquén. Precise localities are given for the first time for the Chilean taxa *Eroessa chiliensis* and *Mathania leucothea* in Argentine Patagonia. *Colias flaveola* is reported for the first time in Argentina. *Colias mendozina*, rediscovered in the highlands of Mendoza, is treated as a full species. Zoogeographic relations among the *puna*, the pampean ranges (Cumbres Calchaquíes — Sierra de Aconquija), the main *cordillera*, the Cordón del Viento, and Patagonia are clarified by the Pierid data. Previous work has overemphasized the distinctness of the Fuegian fauna, whose only important Pierid endemic is the possibly-extinct *Colias ponteni*.

Subspeciation in most genera is probably of Quaternary origin, but speciation and certainly the origin of endemic genera or species-groups antedates the Pleistocene. The existing Pierid fauna represents the current stage in a long and complex process involving dispersal, vicariance, and evolution, the outlines of which are only beginning to emerge. Current distributions reflect both contemporary ecological phenomena and the long-term sequelae of past faunal movements in response to geoclimatic change.

Resumen. La fauna de mariposas Pieridae de los sectores altoandinos y patagónico-fueguinos de la República Argentina fue analizada del punto de vista zoogeográfico — histórico, utilizando muestreos basados en 12 años de colecta por el autor y los registros confiables de diversos museos y colecciones en dicho país, Estados Unidos y Inglaterra, entre otros. La *Tatochila blanchardii* por razones de intergradación espontánea ya se halla subespecie de *T. autodice*. Las taxa *T. arctodice*, *macrodice*, *sterodice*, *vanvolxemii* y *fueguensis* cambian en subespecies de la especie politípica muy ampliamente difundida *T. mercedis*. La ocurrencia de fenotipos muy parecidos a la *Hypsochila* *galactodice* en la puna argentina indica la posibilidad de simpatría con la *H. wagenknechti sulfurodice* en dicha zona, a pesar de la ambiguëdad de la relación de estas "especies" mas al sur. Se aclara la historia muy confusa de la taxonomía del genero *Phulia* en el Cono Sur, y se presenta registros mas australes que los anteriormente conocidos. También se ofrece registros minuciosos de las mariposas chilenas *Eroessa chiliensis y Mathania leucothea* en la Patagonia argentina y de *Colias flaveola* en la cordillera de San Juan por primera vez. La *Colias mendozina*, recien descubierta en la cordillera de Mendoza, se coloca como especie. Se aclaran las relaciones entre la puna, las Sierras Pampeanas, la cordillera, el Cordon del Viento, la Patagonia y la Tierra del Fuego, mostrando entre cosas una enfasis no justificada en el tratamiento de la pieridofauna fueguina, cuya unica especie endemica es la *Colias ponteni*, "perdida" desde 1852.

Para explicar los patrones de especiacion y distribución de dicha fauna hay que desarrollar un esquema historico tomando en cuenta los cambios geofisicos y climaticos del continente y vinculando los ambientes tropicales con los extratropicales y los altos con los bajos. Segun parece la especiacion y seguramente el origen de generos y subgeneros o grupos de especies ha sido anterior a la Pleistocena, aunque la subespeciación, como en la *T. mercedis*, sea fenomeno pleistoceno y/o holoceno. El estado actual de la fauna refleja una historia muy complicada de dispersion y migracion, mezclada con procesos de vicariancia tal que no se puede atribuir todo a ningún solo proceso evolutivo y/o faunístico.

> El cuadro que doy al final de este articulo, sin contener casi nada de nuevo, excepto quiza algunos datos biologicos de poca importancia, tiene por objeto mostrar de un solo golpe de vista ese laberinto en parte desembrollado...demostrar que desgraciadamente nuestros conocimientos sobre las especies del género *Tatochila* son aún muy incompletos....Surge inmediatamente la vieja cuestión: ¿son especies o son variedades? Sabido es que este término *especie* es por demás elástico...[1]
>
> Eugenio Giacomelli, 1915

Introduction

Twenty years ago the lowland tropics were commonly viewed by biologists as a sort of museum of living fossils, persisting untouched through the ages while the biota of higher latitudes was decimated and reinvigorated by the geoclimatic catastrophes of the Quaternary. Academic discussions of the causes of tropical biotic diversity — which typically meant tropical lowland rainforest biotic diversity — were very popular in the 1960s. In this context, the "geologic time hypothesis" claimed that a vast flow of time uninterrupted by disaster had allowed biotic richness to accumulate unencumbered in low latitudes. That view was later stood precisely on its head. By the 1980s the "refugial hypothesis" had become the conventional wisdom: the tropical forest had been fragmented repeatedly in the Quaternary, dividing populations and promoting speciation. Instead of stasis, the tropics were now seen to be in a state of perpetual dynamism; instead of antiquity, species were now seen as manifestations of the recent past — an equally erroneous view, as subsequent events have shown.

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[1] "The chart which I give at the end of this article, without containing anything much that is new except a few biological data of little importance, has as its object to demonstrate at a glance this partly-disentangled labyrinth...to demonstrate that, unfortunately, our knowledge of the species of the genus *Tatochila* is yet very incomplete...The old question immediately arises: are they species or varieties? It is known that this term *species* is, moreover, elastic..."

The locations of proposed Quaternary refugia in the tropical lowlands are inferred from contemporary biological phenomena, such as the geographic distribution of endemism and of zones of intergradation or hybridization (the two are not necessarily the same). Extremely little paleoclimatic information is available for the lowland tropics, primarily because suitable depositional environments for pollen and other fossils are rare (cf. Liu and Colinvaux 1985, 1988). To a degree which can be embarrassing to some of its practitioners, the refugial theory is pegged to climatic reconstructions in the Andean highlands (where excellent palynological records abound) (Shapiro 1989a). At present there are no satisfactory dynamic climate models incorporating orographic effects which relate the highlands to the tropical forests, permitting a test of refugial scenarios derived from present distributions. Progress is being made in refining the existing crude models (Manabe and Hahn 1977, Rind and Peteet 1985), but until they are much better this will remain an important structural weakness of refugia as a purported synthetic theory.

The asymmetry in paleoclimatology is mirrored in biogeography: there have been few in-depth studies of highland organisms, and our knowledge of their distribution is proportionately poorer than in the lowlands. Published distribution maps create a false impression of good coverage. On closer inspection one typically finds the dots are distributed along the major trans-Andean highways. One of the first efforts to correlate animal speciation and distribution in the Andes with Quaternary climatic dynamism was by Adams (1973, 1977) and Adams and Bernard (1977, 1979, 1981), working on the pronophiline Satyrid butterflies of the Colombian and Venezuelan Andes and nearby ranges. But Adams merely suggested a mechanism for speciation — a plausible and quite conventional one — and was unable to correlate specific species with specific geohistorical events, since most of the relevant palynology had not been published yet. Indeed, there is nothing in Adams' work which enables us to differentiate between geoclimatic dynamism and contemporary ecological forces to account for the pattern of narrow altitudinal ranges and serial species replacement along transects which is characteristic not only of Pronophilini but of tropical organisms generally (Stevens 1989). A decade has passed, but little progress has been made; most of what is being said about high-Andean organisms remains at the arm-waving stage. Nonetheless, the importance of the problem of high-altitude tropical biogeography has been recognized. It has even led to the publication of not one but two attempts at synthesis, however premature (Whitmore and Prance 1987, Vuilleumier and Monasterio 1986).

Basically we are asking whether it is possible to find an unmistakeable footprint of the Quaternary in the geography of the high-altitude biota, when we have paleoclimatic reconstructions from the immediate neighborhood. If not, the prospects of validating lowland scenarios with highland paleoclimatology look especially bleak. But we are also asking whence comes the highland biota and how old it is. This is a different and largely independent set of questions, because taxonomically the high-Andean biota has remarkably little connection with the tropical lowlands nearby.[2] Indeed, the taxonomic decoupling of high and low altitudes in the Neotropics is such a striking phenomenon that it seems as if it *must* bear on the geologic evolution of the region and have important implications for how we look at the problem of diversity — even if no one has any idea what they might be. Chabot and Billings (1972) addressed the question of how high-altitude floras originate, using the geologically young and relatively isolated Sierra Nevada of California as their example. They found a small floristic contribution from circumpolar-boreal sources. The principal source was the adjacent Great Basin, and they were able to identify physiological adaptations to the Great Basin climates which preadapted species to enter the alpine as it appeared. But the principal geographic sources of the high-Andean biota are in many cases not in adjacent climates but in another hemisphere, raising special and very interesting problems (Van der Hammen and Cleef 1987, p. 159). Raven and Axelrod (1974) attempted to assess probable antiquity of the various Andean plant families (and make Crucifers, hosts of most Pierini, quite late — late Miocene-Pliocene — though Tropaeolaceae were clearly there earlier and probably evolved there).

Among the Andean butterflies the Pierids have distinct advantages for biogeographic study. Their diversity is great enough to be interesting and quantifiable, but not so great as to be overwhelming. (Ultimately the Andean Theclines, with their high diversity, may be the most informative butterfly group. However even their generic-level taxonomy remains fluid, many taxa are undescribed, and distributional data are fragmentary at best.) The Pierids are medium-sized, conspicuous, often easily reared, and not prone to cryptic speciation. They are the most conspicuous element of most high-Andean butterfly faunas: most of the common, widespread species are Pierids (and they were commented upon by many early travelers, such as Whymper (1892)). Their colors and patterns, as noted by Descimon (1986), are comfortably familiar to biologists of Holarctic origin, the product either of common ancestry or striking convergence — as usual, posing the problem of telling the difference. Most of these factors were noted by the end of the last century. Unsatisfactory as it is, it is not accidental that the Andean Pierid literature is better (richer) than that of any other high-Andean butterfly group. Descimon (1986) emphasizes the Pierids for all these reasons when he attempts a synthesis of high-Andean butterfly biogeography.

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[2] Descimon, 1986, p. 526 states categorically that "...it is clear that the Neotropical and southern temperate regions contributed little (or nothing) to the oreal butterfly fauna of the Andes. Its affinities lie instead with the Holarctic realm." The dangers in such generalizations have been demonstrated in recent revisionary work on the Argentine Theclini by Kurt Johnson and his coworkers. Johnson finds that the "Andean *Incisalia*" (*Thecla culminicola* group) are "a sister-group of the diverse and primarily montane Neotropical...groups...not an immediate southern relative of cryptically-marked Nearctic *Incisalia*" (Johnson *in litt.*, 7 April 1989). As a cautionary note I mention that *Tatochila* and the Neotropical genus *Ascia* show striking electrophoretic similarities, as well as resemblances in anatomy of the early stages (Shapiro and Geiger, unpublished). If this relationship is real, however, the direction of evolution has not been established.

Another ongoing problem of refugial theory has been its failure to integrate its scenarios for both climate and biogeography in northern South America with the large, powerful and growing body of paleoclimatic evidence from farther south. Among the best-studied regions on earth from a palynological-paleoclimatic standpoint are Patagonia and Fuegia. Moreover, some of the information emerging from them is strongly at variance with the currently conventional wisdom on the geohistory of the continent, particularly the timing of the most important uplift (Clapperton 1983, Mercer and Sutter 1981). The Patagonian and Fuegian butterfly faunas are taxonomically unbalanced (dominated by Satyrids) but not especially impoverished. They are instructive in their apparently very close ties to the faunas of the high central Andes and also in the character and level of their endemisms. They are highly relevant to the interpretation of the Andean faunas as a whole.

The group of endemic pierine genera including *Tatochila* and *Phulia* has been monographed by Field (1958), Herrera and Field (1959), Field and Herrera (1977) and Ackery (1975). This body of work has made the Andean pierines attractive for biogeographic interpretation, as by Brown (1987) and Descimon (1986). But if the data for Pierini are, relatively, unusually good, they are still not very good in the absolute sense. It is possible to extract meaningful inferences from fragmentary data, and perhaps even to arrive at correct scenarios based on them. But one should not count on it Even for Pierids, almost every field trip to the high Andes or Patagonia turns up important surprises; for Lycaenidae or Hesperiidae, such surprises are guaranteed.

This paper draws on both published and unpublished data in an attempt to pull together and analyze the zoogeography and systematics of the Andean and Patagonian Pierid fauna of the Argentine Republic. It calls on field trips undertaken over 12 years, comprising over 18,000 miles of travel on the ground, from the Bolivian border to

Ushuaia, Tierra del Fuego — as well as on the accumulated experience of previous butterfly workers in that country. Argentina comprises an array of biomes ranging from tropical rain forest to cold steppe and periglacial tundra. Northwest Argentina is at the margin of the great Andean *altiplano*, the center of diversity for the miniature Pierids of the *Phulia* lineage, and of the dissected *jalca* or "*páramo*" where *Tatochila* achieves its greatest diversity. The *altiplano* is manifested in the *puna* of Salta and Jujuy and the highest elevations of the *Sierras Pampeanas*, while the "*páramo*" can be seen in, for example, the Cuesta del Obispo and the mid-reaches of the *Sierras Pampeanas*. If Pierid diversity does not quite match Arequipa or Cusco, it is still sufficient to be informative. More importantly, the geography is singularly favorable for tracing the rarefaction of northern (i.e., tropical) lineages as one proceeds southward into temperate climates, and *vice versa*. In so doing, one connects Patagonia and Fuegia to the central Andes at last, within the taxonomic limits set below.

Of the Andean countries, Argentina may not be the most critical in terms of its overall potential contribution to historical biogeography, but it is certainly not the least and it is definitely the easiest. Working out Argentine Pierid faunistics is logistically feasible. Doing the same for Peru or Bolivia, which may have more to say about coupling the highlands and the lowland tropics, is a much more daunting project (barely begun for Peru by Lamas, 1982): the faunas are much richer, there is much less of a data base, and field work is much more difficult. Repeating the task attempted here for Argentina for other countries and other taxa will be a slow, agonizing process, but there is no substitute for it. Perhaps the next attempt at a synthesis of high-altitude tropical biogeography will be shorter on speculation and much longer on hard data where the butterflies are concerned. Perhaps some day there will even be an integrated overview of continental paleoclimates and paleobiogeography for South America, and the butterflies will be a significant group in its preparation.

Defining the Target Fauna

Breyer (1939) provided the first systematic list of Pieridae from the entire Argentine Republic. It reveals a large Neotropical, lowland — lower montane element distributed in the Northeast, the Chaco and the Yungas. Because the affinities of this fauna, as well as its south- and westward limits, are so clear, I have not treated it in this paper. A study like Larsen's (1984) for the Arabian Peninsula, which seeks to identify the relative contributions of different source regions to a "crossroads" fauna, is particularly interested in such things as the tropical-temperate transition alluded to here. But the taxa of *Phoebis*, *Eurema*, *Zerene*, *Anteos*, *Leptophobia*, *Perrhybris*, *Pereute*, *Appias*, *Catasticta*, *Hesperocharis*, *Dismorphia*, *Pseudopieris*. . . barely if at all impinge on the objectives of this paper. Of the group of long-range migrants, *Eurema deva* Dbl. and *Colias lesbia* Fabr. have been included because they penetrate (and breed seasonally) so far into the middle latitudes, while *Phoebis sennae* L. and *Ascia monuste automate* Burm. have been excluded because they rarely penetrate south of Buenos Aires. *Theochila maenacte* Bdv. poses a unique problem. It does not appear in the analyses because it is confined to lowlands in the Northeast, south to greater Buenos Aires. But it is discussed in the text because of its close phylogenetic relationship to *Tatochila* and its broader biogeographic import. *Teriocolias* also poses a problem. It is a montane insect whose seasonal cycle includes regular up- and downslope movements which make it a component of the highland fauna. On that basis it has been included in the analyses, and a few new data are reported (cf. Schaefer and Breyer 1941).

After all these somewhat arbitrary decisions, the fauna comprises: all the Argentine taxa of the genera *Phulia*, *Hypsochila*, *Tatochila*, *Eroessa*, *Colias* and *Teriocolias*, plus *Mathania leucothea* Mol. and *E. deva*. The concluding analysis incorporates Chilean data, adding a few taxa of the above genera plus *Infraphulia ilyodes* Ureta, *Pierphulia rosea* Ureta (two subspecies) and *P. isabela* Field and Herrera — any of which might still turn up in the poorly-collected *puna* of far NW Argentina.

Phytogeographical Analyses of Argentina: an Overview

Argentina has a venerable tradition of ecology and natural history and an extensive domestic literature in Spanish, which is largely unknown outside the country. There have been several comprehensive attempts to schematize the ecobiogeography of Argentina, one of which (Shannon 1927) actually emphasized entomological considerations. The majority, however, are concerned with climate and plant communities (taxonomically defined) or formations (physiognomically). In 1953(a) Cabrera summarized and attempted to synthesize these. He updated this work in 1971; what follows is largely abstracted from that paper (Fig. 2), but with some input from Castellanos and Pérez Moreau (1945), Sarmiento (1975), Hueck and Seibert (1972), Cabrera and Willink (1980), Davis (1986) and Irwin and Schlinger (1986) with additional from Gómez Molina and Little (1981) on mountainous regions and Correa Luna *et al.* (1977) for the National Parks. Figs. 3–5 are from Madsen *et al.*, 1980, redrawn and should be used in conjunction with Cabrera. Given the montane-austral focus of this paper, the lowland tropics and subtropics are not discussed below.

Cabrera divides Argentina into two regions, five domains, and 13 provinces, as follows; those marked * are discussed in more or less detail in this paper:

I. Neotropical Region
    A. Amazonian Domain
        1. Yungas Province*

        2. Paraná Province
    B. Chaco Domain
        3. Chaco Province
        4. Espinal Province
        5. Prepuna Province*
        6. Monte Province*
        7. Pampa Province
    C. Andean — Patagonian Domain
        8. High-Andean Province*
        9. Puna Province*
        10. Patagonian Province*
II. Antarctic Region
    A. Subantarctic Domain
        1. Subantarctic Province*
        2. Insular Province
    B. Antarctic Domain

Many of the habitats described below are illustrated in Plates I–IV.
Yungas Province. The Yungas occupy a narrow altitudinal belt on the eastern slopes of the mountains lying in or just barely beyond the tropics in northern Argentina, from roughly 500 to 2500 m above sea level. They extend far N into Bolivia, and S only to the north of Catamarca in the Pampean Sierras (Sierra de Aconquija), but including all the ranges in Tucumán. The climate is warm and humid, with most of the rain falling in summer. Precipitation ranges locally from 700 to 2500 mm or more, with very pronounced orographic effects. Mean annual temperature also varies greatly: from 14 to 26°C. A great variety of microclimates thus exists. Winter frosts occasionally occur at lower elevations and are common higher, where heavy snow may fall several times a year. In the tropics there is no true winter, and any snow that falls at these altitudes does not persist.

The predominant vegetation is cloud forest, with trees reaching 30 m in height and abundant lianas, epiphytes, and a dense understory of herbs and shrubs. Various transitions from such vegetation to desert, steppe, shrub-steppe, and temperate deciduous forest occur; ecotones may be gradual or abrupt, the latter usually reflecting rain shadows or the altitudes of semi-permanent inversions. Some of the most dramatic vegetational transects in South America may be made here, particularly in Tucumán. Cabrera divides the Province into three Districts, viz.:

(a) *Transitional Forest.* This is the transition from Yungas to Chaco, occurring from Pocitos to Orán in northern Salta; on the E flanks of the Sierras Maíz Gordo, Centinela and Santa Bárbara, etc. in Jujuy, the valley of Lerma and the mountains of Metán and Rosario de la Frontera again in Salta, the lower slopes of the Sierra de Medina and the Aconquija-Calchaquíes ranges in Tucumán. Temperatures are high but precipitation relatively low (700–1000 mm), and deciduous trees, especially rather small Leguminosae, predominate.

(b) *Mountain Forest.* This narrow belt occurs above the preceding, reaching up to 1300 to 1800 m. It is very rich floristically and faunistically and commonly includes the southernmost populations of many lowland-tropical organisms on the continent; this is the so-called *selva Tucumana.* Precipitation is from 1500–2500 mm or locally higher; temperatures within the forest are cool in the intense shade and, frequently, in cloud and mist. Characteristic of this forest is the *horco molle* tree, *Blepharocalyx gigantea*, but many other conspicuous tree species occur. Butterfly species richness here is similar to that observed in the warm, humid far NE of Argentina.

(c) *Mountain Woodland.* This is the uppermost stratum of the Yungas and marks the transition from Mountain Forest to the treeless formations of the high mountains. Some characteristic woody species are *Podocarpus parlatorei*, alder (*Alnus jorullensis* var. *spachii*), elderberry (*Sambucus peruviana*), *Schinus gracilipes*, etc. with local outliers of *quenoa* (*Polylepis australis*) generating a spotty second treeline above 2500 m in some locations (Fernández 1970). The woody flora includes both Holarctic and Subantarctic elements. The herbaceous flora is very rich and includes many showy wildflowers, largely of Holarctic origin. The higher meadows — as between Tafí del Valle and Abra Infiernillo — include many perennial bunchgrasses. Above 2000 m trees are often confined to creek bottoms. Meadow and brush vegetation may occur much lower, however, as on the Cumbre de San Javiér near San Miguel de Tucumán, and it is unclear whether this reflects the well-known "telescope effect" found in tropical mountains or the medium- to long-term consequences of land use. Similar vegetation occurs at the highest elevations of the Sierras of Córdoba, representing a far-southern outlier of the Yungas.

Prepuna Province. This is the vegetation of the dry slopes and canyons from Jujuy to La Rioja, mainly between 2000 and 3400 m, but locally down to 1000 m in certain microclimates. It intervenes between the uppermost Yungas and the true *Puna*, but also between the Chaco and the *Puna* or the Monte and the *Puna*. The climate is warm and dry, with rain exclusively in summer thunderstorms. The vegetation is xerophytic shrub-steppe with aspect dominance by columnar cacti, of which *Trichocereus pasacana* and *T. terscheckii* are typical in the N and S respectively. Terrestrial Bromeliads and shrubby Leguminosae abound. Common genera include *Adesmia*, *Azorella*, *Junellia*, *Mulinum*, *Nassauvia*, *Parastrephia* and *Senecio*. Riparian woodland occurs in canyon bottoms, with *molle* (*Schinus areira*) and *chilca* (*Baccharis salicifolia*). Because of its complex geography, *prepuna* has little distinctive butterfly fauna and indeed is often rather depauperate, though it occasionally serves as a corridor to bring higher-altitude species lower and *vice versa*, in butterflies as in plants. A major reference is Hunziker (1952).

Monte Province. The *Monte* begins in the valley of the Río Santa María in the Valles Calchaquíes, extending S through the W of Tucumán and La Rioja, through Mendoza and San Juan and thence into Neuquén and the E of Río Negro and in dilute form even to far NE Chubut. Precipitation varies from 80–250 mm (locally higher), mean temperature from 13–17.5°C, with pronounced climatic gradients both E–W and N–S. The vegetation is desertic and diverse, but dominated throughout by creosote bush (*Larrea* spp.) and mesquite (*Prosopis* spp.) except in alkali sinks, where *Distichlis* and Chenopods predominate. Common genera include *Bougainvillea*, *Bulnesia*, *Caesalpinia*, *Cassia*, *Cercidium*, *Mimosa*, *Trichocereus* and *Zuccagnia* and in gullies *Acacia* and *Celtis*. The *Monte* corresponds ecologically to the Sonoran Desert of North America, and like it segues almost imperceptibly into adjacent colder formations. Large-scale comparisons of community organization and function were made between the *Monte* and the Sonoran Desert as part of the International Biological Programme and are summarized in Orians and Solbrig, 1977.

Pampa Province. This is the bunchgrass prairie ofArgentina, much of it now degraded and invaded by exotic weeds. It occurs at low to moderate elevation in flat to rolling country in the E, roughly between 31–39°S. There are pronounced climatic gradients, particularly in precipitation, from 1100 mm in the NE ("subhumid *pampa*") to 600 mm in the SW ("subarid *pampa*"). The various floristic subdivisions are unimportant for this paper. The butterfly fauna has surprisingly low endemism.

The Andean – Patagonian Domain: General Considerations. The following translation from Cabrera (1971, p. 29 ff.) captures the character of the Domain well: "In the Argentine Republic this Domain extends all along the extreme W of the country, covering the *puna* and the Andean *cordillera* from the border with Bolivia to the S of Mendoza. There it begins to reach out to the E on the mesetas and the Patagonian ranges, reaching the Atlantic in Chubut and Santa Cruz. Its climate is cold and dry, with frosts almost all year and snow in winter. The Andean-Patagonian Domain is characterized by the scarcity of endemic families (of plants), only the Malesherbaceae and Nolanaceae being exclusive to it, and in turn a great richness of endemic genera of the most diverse groups. The families of greatest importance for their richness in genera and species are the Composites, Grasses, Verbenaceae, Solanaceae, Cruciferae, etc. The Legumes are represented by few genera, principally Papilionaceous, but at times with numerous species, as in *Adesmia* and *Astragalus*. The Zygophyllaceae and Mimosoid Legumes, so abundant in the Chaco Domain, are almost completely lacking. The dominant vegetation is shrub- or herbaceous steppe, with extreme forms of adaptation to wind and drought...Where springs exist or water accumulates, inundated meadows form, called *vegas* in the *cordillera* and *mallines* in Patagonia." Cabrera gives a detailed subdivision of the Domain.

High-Andean Province. Again from Cabrera 1971, p. 30: "From the border with Bolivia to Tierra del Fuego. In Jujuy and Salta found approximately above 4400 m; in Mendoza above 3000, in Neuquén and Río Negro above 1600 m and in Tierra del Fuego above 500 m.... Immature, rocky or sandy soils, with a high-montane climate, cold and dry (except in the S), with snow or hail at any time of year. The mean temperature is low, below 8°C (−1.5°C at Crísto Redentor, Mendoza, at 3829 m). The vegetation is very poor and is formed by grassy steppe or steppe of cushion chamaephytes..." Three Districts are recognized, which are very important for understanding the butterfly fauna:

Quichua District. This is the true high-Andean vegetation, occupying the Eastern, or Royal Cordillera S to the N of San Juan from 4300–5600 m. It is thus tropical and subtropical. Precipitation is higher in the N and E, where the District contacts the Yungas and Chaco, than in the S and W where it contacts the Monte. It is strongly seasonal, concentrated in afternoon thunderstorms during the "Bolivian Winter" from November to February caused by the S-ward migration of the Intertropical Convergence Zone in response to heating in the continental interior. The most common climax formations recognized by Cabrera are: *Festuca orthophylla* – *F. chrysophylla* – *Poa gymnantha* steppe, with such associated spp. as *Stipa* and *Deyeuxia*, *Baccharis incanum*, *Senecio graveolens*, *Werneria poposa*, *Adesmia caespitosa* and *patancana*, and the remarkable *yareta*, *Azorella compacta* (Umbelliferae), a cushion plant formed of thousands of tiny terminal rosettes; also smaller, delicate wildflowers including *Perezia ciliosa*, *Silene friesii*, *Cajophora coronata*, *Calceolaria glacialis*, *Valeriana spathulata*, *Nototriche anthemidifolia*, etc.; steppe of vizcacha grass (*Stipa frigida*) with shrubs such as *Artemisia copa* and *Senecio viridis*; Bitter Coirón (*Stipa chrysophylla*) — vizcacha grass steppe associated with the dwarf Leguminous shrubs *Adesmia glanduligera* and *A. nanolignea*; and others. Some additional characteristic or indicator species are: among the cushion plants, *Oxalis compacta*, *Senecio algens* and *Pycnophyllum molle*; very high-altitude Crucifers (*Aschersoniodoxa mandoniana*, *Parodiodoxa chionophylla*, both reaching above 5000 m); sedges of inundated *vegas* (*Oxychloe andina*, *Carex incurva*, *Scirpus atacamensis*), often with grasses (*Deyeuxia* spp., *Festuca scirpifolia*); the dwarf rush *Distichia muscoides*, and showy wildflowers including *Gentiana prostrata*, *Gentianella punensis*, *Calandrinia acaulis*, *Werneria pygmaea*, and many *Astragalus* spp. This is a flora closely allied to that of the highlands of southern and central Peru (Weberbauer 1945).

Cuyo District. This is the vegetation of the high Andes of San Juan, Mendoza and the N of Neuquén, from 4500 to 2200 m descending southward. The winters are very snowy; total preciptation is highly variable but always includes summer thunderstorms. The District is entirely outside the tropics and beyond the influence of the "Bolivian Winter," being dominated instead by the interplay of tropical and subantarctic air masses with traveling storms and fronts. Coirón (*Stipa* spp.) is a climax aspect dominant in much of the District, often associated with perennial *Festuca* and *Poa*. The dominant species of *Stipa* varies geographically. On steep slopes shrubs are common, including *Adesmia pinifolia*, *Ephedra andina*, *Berberis empetrifolia*, *Senecio uspallatensis*, *Mulinum ovalleanum*, etc. Typical herbaceous species include *Menonvillea cuneata*, *Nassauvia lagascae*, *Tropaeolum polyphyllum*, and, in *vegas*, the dwarf rush *Andesia bisexualis*, *Plantago barbata*, and *Senecio breviscapus*. Streams are often bordered by *Cardamine nivalis* and there may be a turf of *Hordeum secalinum* or *Agrostis glabra* with *Hypsela oligophylla* and *Werneria pygmaea*. The classic description is by Hauman (1919). A useful modern treatment of the flora is Wingenroth and Suárez (1983).

There is a remarkably rapid floristic and vegetational gradient from N to S in the *Cuyo*. The northern part of the *Cuyo* forms a transition from the tropical climates to the N, dominated by rainfall seasonality but with no true winter, to the strongly temperate-seasonal climates in Mendoza with a pronounced winter snow pack. By the latitude of Las Leñas and Cerro Sosneado the climates and aspect have become decidedly more Patagonian. These gradients are reflected from the high desert to the high alpine in the presence of species-level endemics among flowering plants and butterflies. Because of its easy accessibility, the vicinity of the Paso Bermejo is often taken as "typical" of the montane *Cuyo*, thereby underestimating the high diversity within the District.

Austral District. From C and SW Neuquén southward at ever-decreasing elevation, the high-Andean flora descends and mixes with Gondwanaland (subantarctic) elements, especially in the more humid areas. Steppes are often dominated by *Poa obvallata* and *Festuca weberbaueri* or *F. monticola*, the marshy meadows by *Deyeuxia*, *Deschampsia*, and *Poa*, and especially in the far S, crowberry (*Empetrum rubrum*) becomes conspicuous or dominant on poor (sandy, sterile, and boggy) sites. The communities of Tierra del Fuego, which partake of this District but also of the Subantarctic Domain, are well-described in Moore (1983).

Puna Province. The Argentine *puna* occurs from 3400 to 4500 m, from the Bolivian border to NE Mendoza, where it can be found in dilute form to 2000 m. The climate is dry and cold, with mean annual temperature of 7.5–9.9°C and annual precipitation from 324 mm at La

Quiaca to 103 mm at San Antonio de los Cobres, to nearly zero at the Chilean border.

The *puna* is a xerophytic high-altitude shrub-steppe dominated by *tola* (*Parastrephia lepidophylla*) and river *tola* (*P. phylicaeformis*) where ground-water levels are fairly high. Many other species occur (*totilla, Fabiana densa*; *chijua, Psila boliviensis*; *anagua, Adesmia horridiuscula*; etc.) along with dwarf cacti (*Opuntia soerensii, Oreocereus trollii*, etc.). Some other characteristic species are *Pennisetum chilense, Scirpus atacamensis, Juncus depauperatus, Plantago tubulosa, Hypsela oligophylla, Festuca scirpifolia, Bouteloua simplex, Muhlenbergia fastigiata, Trifolium amabile, Astragalus bustillosi, Ipomoea minuta*, etc. Farther W, in Chile, extensive flat bogs occur within the *puna*. The classic description is Cabrera's (1958) monograph.

Comment on the High-Altitude Vegetation in Salta, Jujuy and Tucumán. — The Argentine NW is vegetationally very complex, as Figs. 6 and 7 demonstrate. The upper reaches of the Yungas grade into *prepuna, puna*, and Quichua high-Andean vegetation and the formation is exquisitely dependent on slope, exposure and in some cases, substrate. As noted below, many of the high-altitude butterfly species appear to have very specific requirements within this complex mosaic, but may be widespread where their particular microclimates occur. This is characteristic of tropical organisms, while temperate species tend to be more broadly distributed both ecologically and geographically (Stevens 1989). A notable exception is *Tatochila mercedis macrodice*, which seems to transcend formation or association boundaries, occurring nearly everywhere at high altitude.

Patagonian Province. The first hints of Patagonian vegetation appear in the *precordillera* of Mendoza. The transition from the *Monte* and *Cuyo* to Patagonia occurs gradually from Chos Malal, Neuquén S through Loncopué to Zapala. In the N of this transition zone the *mallines* are nearly or quite pure Patagonian while the nearby hills have an increasing proportion of Patagonian species with both latitude and altitude.

The traditional "political" boundary of Patagonia is the Río Negro, but Patagonian floristic elements occur N in the W of the region, while elements of the *Monte* reach even beyond Comodoro Rivadavia on the Atlantic shore. The precise location of the boundary of the Patagonian Province is controversial (cf. Soriano 1949, 1956, Ragonese and Piccinini 1969). Soils are sandy or gravelly — much of the Province is covered with a thin pavement of gravel washed out from the glaciers — and the climates are cold and dry with winter snow, frosts much of the year, and very persistent strong winds which are perhaps the most characteristic feature. The temperature varies from an annual mean of 13.4° at Chos Malal to about 5° at Río Grande, NE Tierra del Fuego;

precipitation ranges from 100–270 mm over the Patagonian steppe, but rises very rapidly to the W as the continental divide (=border with Chile) is approached. The dominant plant communities are shrub-steppe and bunchgrass steppe. Cabrera recognizes six Districts (but see Boelcke 1957):

Payunia District. This is the *Monte*-Patagonia ecotone in the far N, characterized by *solupe* (*Ephedra ochreata*), the composite *Chuquiraga rosulata*, *Lycium chilense*, *Grindelia chiloensis*, *Junellia seriphioides* and, locally in cool sites, *neneo* (*Mulinum spinosum*), the most distinctively Patagonian element. The unusual Umbellifer *Hydrocotyle*, of subtropical origin, occurs along slow streams — its only occurrence in the Province.

Western District. This is a narrow fringe of shrub-steppe, from northern Neuquén to NE Santa Cruz, dominated by *Mulinum spinosum*, *Trevoa patagonica*, *Colliguaya integerrima* and *Nassauvia axillaris*, with local *coironales* (bunch-grass prairies) of *Stipa humilis*, *neaei* and *speciosa* often containing *Poa huecu*, *Bromus macranthus*, *Festuca argentina*, etc., and more or less saline seeps or marshes with *Distichlis scoparia* and *D. spicata* and bulrush marshes (*Scirpus californicus*). Pampas-grass (*Cortaderia* spp.) reaches its southern limits here, often in overgrazed bottomlands just upslope a few cm from *mallines* of *Distichlis*.

Central District. This is the most arid part of Patagonia, from the center of Río Negro through most of Santa Cruz. The predominant steppe species are *quilenbai* (*Chuquiraga avellanedae*), *colapiche* (*Nassauvia glomerulosa*), and *coirón amargo* (*Stipa humilis*, *neaei* or *speciosa*); associates include *Ameghinoa patagonica*, *Nardophyllum obtusifolium*, and *Brachyclados caespitosus*. In the far S, *quilenbai* drops out and is replaced by *mata negra*, *Junellia tridens* (Verbenaceae, not to be confused with other shrubs having the same common name in other regions). Saline marshes are dominated by *Atriplex lampa*. In moist gullies larger shrubs such as *Anarthrophyllum rigidum*, *calafate* (*Berberis cuneata*), *Senecio filaginoides* and *Lycium chilense* occur.

San Jorge District. This is a “warm pocket” along the Gulf of San Jorge in the vicinity of Comodoro Rivadavia, where *Monte* elements including creosote bush can be found. Characteristic dominants are *Trevoa patagonica*, *Colliguaya integerrima*, *Stipa humilis*, *Mulinum spinosum*, *Adesmia campestris*, *Anarthrophyllum rigidum*, *Festuca pallescens* and *argentina*, etc.

Subandean District. This is the lower fringe of the Patagonian Andes proper, widening out S of 51° to reach the Atlantic. Annual precipitation is 200–350 mm; the climate is humid at least part of the year, even the dry season is rather cloudy due to high-altitude moisture transported over the Andes by the prevailing westerlies and formed into extensive wave altocumulus in their lee, and the soils are richer and more mature than in areas further NE. The climax vegetation is *Festuca pallescens* steppe, with a very long list of associates including *Poa ligularis*, *Bromus macranthus*, *Elymus patagonicus*, *Calceolaria polyrhiza*, *Acaena pinnatifida*, *Viola maculata*, *Lepidophyllum cupressiforme*, etc.

Fuegian District. This is the NE of Tierra del Fuego, extending to the transition from steppe to *Nothofagus* forest SW of Río Grande. *Festuca gracillima* is the dominant steppe grass. Many characteristic and showy wildflowers occur, of which *Primula magellanica* and *Oxalis enneaphylla* and *fueguensis* are characteristic.

Subantarctic Domain and Province. Characterized by the dominance of south-end-of-the-world (Gondwanaland) taxa of great antiquity, adapted to cool and moist, temperate climates — *Nothofagus*, *Dacrydium*, *Fitzroya*, Myzodendraceae, Desfontainaceae, Tetrachondraceae, Donatiaceae, etc. This Domain is mainly W of the Andean crest in Chile. Four distinct Districts are recognized by Cabrera; their relationships are clearer when the vegetation map of Chile is consulted along with that of Argentina.

Pehuénia. The relict forests of Pehuén, *Araucaria araucana*, from Volcán Copahue to Lake Lolog in western Neuquén, from 900–1800 m, associated with *Nothofagus pumilio*, *Chusquea culeou*, *Berberis buxifolia*, *Pernettya mucronata*, *Maytenus disticha*, *Ribes magellanica*, *Escallonia virgata*, *Nardophyllum obtusifolium*, *Cortaderia pilosa*, *Chlorea alpina*, *Acaena pinnatifida*, etc. — marking the N limits of many species, and diluting gradually to the E in the San Martín–Junín–Aluminé region until only occasional *Araucaria* are superimposed on bunchgrass steppe; such sites are often called "Primeros Pinos."[3]

Deciduous Forest District. The forests of *Nothofagus pumilio* and *antarctica* and of *Austrocedrus chilensis* extend to tree-line above and steppe below, with a complex structure of communities or associations. In the far N *Nothofagus procera* and *obliqua* also occur. The *coligüe* bamboo, *Chusquea culeou*, is locally very abundant, as on Cerro Catedral near Bariloche. Wildflowers are numerous and include *amancay*

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[3] The easternmost stand of *pehuenes* is located on the Espinazo del Zorro along Highway 46, SW of the Laguna Blanca National Park in Neuquén. It very clearly indicates a much more mesic climate eastward within the past 1000 yr or so. The genus *Araucaria* was formerly much more widespread, both globally and in South America, and has been in decline since the early Tertiary. The Olsacher Museum of Geology in Zapala, Neuquén has an excellent collection of fossil *Araucaria* material from the region. The complete lack of a distinctive butterfly fauna associated with the *pehuén* vegetation is striking.

(*Alstroemeria aurantiaca*), *Codonorchis lessonii*, *Mutisia spinosa* and *decurrens*, etc. Like the preceding, this District is defined by relicts whose distributions reflect very local, topographically-mediated microclimates E of the crest.

Valdivian District. This is the true cool-temperate Tertiary rainforest of S Chile, floristically extremely rich but dilute on the Argentine side of the border where it penetrates only in the far W of the Lanín, Nahuel Huapí, and Los Alerces National Parks. Precipitation in some places reaches 4000 mm/yr. It has two characteristic butterflies: the Pierid *Eroessa chiliensis* and the Hesperiid *Argopteron aureipennis* Butl. See Ringuelet (1955).

Magellanic District. The southern beech forests (*Nothofagus*) and associated *Sphagnum*-bog (*turbal*) habitats of Tierra del Fuego (Moore 1983).

Comment on the Vegetation of Patagonia and Fuegia. These parts of Argentina have engendered an immense literature. Besides Cabrera, an excellent overview in English, with comparisons to North America, is to be found in Beetle (1943). Dimitri (1962) reviews the flora, and (1972) sets it in a regional and physiological context.

Cabrera's classification and mapping are necessarily somewhat typological. Even so, it is evident that the Districts are not very well-defined and the lines demarcating them are at best approximations of statistical changes in community composition. The intimate interdigitation of subantarctic and Patagonian elements makes line-drawing in the far S quite arbitrary. My experience suggests that the distribution of Satyridae in Patagonia may be studied profitably with respect to plant community patterns. The Patagonian and Fuegian Satyrids have been monographed by Heimlich (1972).

Among numerous accounts of Patagonia, Lista (1896a, b) and Willis (1914) are particularly instructive in enabling us to assess the amount of vegetational change due to the activities of the white man. It is quite evident, especially from Willis, that the extent of *Nothofagus* forest has been greatly reduced by cutting, burning and conversion to pasturage. Given that many evolutionarily interesting and important phenomena are today occurring in zones where such conversion occurred in the last century, it is important to keep this in mind. The W of Neuquén and Río Negro and the vicinity of the Gulf of San Jorge rank with the W of Salta and the *Sierras Pampeanas* as regions of special concern for butterflies; the mainland-Fuegian transition, in particular the littoral from Comodoro to Río Grande, will also require further attention. Very rapid urban growth in the far S since 1970 is already impacting butterfly habitats.

Systematic Treatment

Collection abbreviations are identified in the Acknowledgments section.

Genus *Theochila* Field

Theochila maenacte Boisuval

Theochila is probably the sister-genus of the non-Crucifer-feeding part of the large genus *Tatochila*, which will almost certainly be divided in two or three genera once sufficient species have been reared. *Theochila* is defined by a variety of odd autapomorphies (Field 1958). The single species *maenacte* is divided into two allopatric subspecies. Its distribution (Brown 1987, Fig. 4.18) is part of a repeating pattern of faunal and floral connections between the Andes and Serra do Mar/SE Brazil, which "leaves no doubt that links of suitable vegetation and humid temperate climate existed across northern Argentina in the distant past" (Brown 1987, p. 95; O. Mielke, pers. comm.).

The nominate subspecies *T. m. maenacte* differs from the Brazilian *T. m. itatiayae* Foetterle primarily in slightly smaller size and a drastic reduction in the dark wing-pattern in the male, producing an effect not unlike *Pieris rapae* L. Herrera and Field (1959) had little material available and apparently did not recognize that *T. m. maenacte* is seasonally diphenic, with a winter form nearly indistinguishable from *itatiayae* and a very pale summer form on which their redescription was based. The BM contains a very extreme winter male, unfortunately without date, labeled "Buenos Ayres, Elwes 1920." It also has a long series of more or less typical summer specimens labeled "Buenos Aires (Belgrano), 15.XII.1889." The very pronounced seasonal polyphenism of the male and lack thereof in the female (in which the denser thoracic and abdominal pelage, and richer black color in the wing pattern are the only manifestations) parallels the situation in *Tatochila vanvolxemii* = *T. mercedis vanvolxemii* Capronnier. It would be of great interest to determine whether photoperiod or temperature or both influence the polyphenism.

Theochila m. maenacte was formerly common in riparian and marsh habitats in and around Buenos Aires (Riachuelo; Avenida de los Italianos — Zona Portuaria, etc.) but has disappeared or diminished in many sites in the past decade. Until slum clearance and construction of the central bus station destroyed its habitat, it was common behind the Retiro railroad station several blocks from the center of the city, as late as the mid-1970s. It was not found in the "Vida Silvestre" preserve in the Zona Portuaria in XI.–XII.1989. It is still common in marshy sites in Quilmes and south to the vicinity of La Plata, which seems to be its southern limit. The Museo de La Plata contains much local material, e.g. series from La Plata, 27.III.1927; 3♀, 2.XII.1928; an extreme winter form ♀, 28.X.1928, and a dozen from the northern suburb of Punta Lara, II. 1928, *leg.* R. Maldonado. It is also still locally common in Tigre and the Paraná Delta north of the capital, and should be looked for in the marshes near Ezeiza (the old "Belgrano" locality?)

Genus *Tatochila* Butler

As noted under *Theochila*, this genus appears to be polyphyletic and will probably need to be divided. At present it is the largest Pierine genus on the continent. Since the lines of the division are not yet clear, I am opting for taxonomic conservatism by retaining all of Herrera and Field's (1959) species-group designations within *Tatochila*, whose type-species is *autodice* Hübner.

Tatochila theodice theodice Boisduval (Fig. 8A, D).

The N and S limits of the nominate subspecies have been poorly defined in Argentina. Herrera and Field (1959, p. 478) had little Argentine material available.

3♂ Loncopué, Neuquén, 8.XI.1988 (AMS)
1♂ Catan Lil, Neuquén, 840 m, 16.I.1977 (MG)

The Loncopué record (38°04′S, 70°37′W) probably defines the N limit of both the subspecies and species as it is unrecorded at Chos Malal, which I have collected very thoroughly. The Catan Lil record may represent the farthest E and downslope penetration of the high desert in river bottoms, to which this mesic species is largely restricted in the N of its range. It is clearly resident at Loncopué, and the specimens are of the early spring (post-diapause) phenotype.

The S limit is defined by the transition to ssp. *gymnodice* Staudinger, which is accomplished in gradual, clinal fashion, as demonstrated by the following material:

2♂ 3♀ Lago Argentino, Península Magallanes, Santa Cruz, loc. #28, 11.I.1979 (DE)
6♂ Tecka, Corcovado, Chubut, 750 m, loc. #47, 17.II.1979 (DE)
1♂ La Esperanza, 130 km NW Río Gallegos, Santa Cruz, loc. #30, 15.I.1979 (DE)

Herrera and Field had no material between the Nahuel Huapí National Park, Río Negro (nominate *theodice*) and Río Túnel, Santa Cruz (*gymnodice*), creating a false impression of disjunction. In the Lago Argentino series the females are somewhat more *gymnodice*-like than the males. See Fig. 8B, E.

Tatochila theodice staudingeri Field

Herrera and Field (1959) divide the Fuegian *theodice* into two subspecies, recognizing *gymnodice* from Porvenir, Magellanes (Chile) and *staudingeri* from Puerto Harberton (the type locality) and Ushuaia, both in Argentine Tierra del Fuego, as well as from Isla Navarino, Magallanes. Again, when sufficient material is assembled, the distinctness of these subspecies disappears.

2♂ 2♀ Cabo Peñas, Depto. Río Grande, T. del F., 17.XII.1983 (ML)
56♂ 30♀ Río Grande, T. del F., 25.XI.1988 (AMS) (Figs. 8C, F)
2♂ Estancia María Cristina, Route 3, T. del F., 27.XI.1988 (AMS)
1♂ 1♀ Base of Monte Susana, Parque Nacional, T. del F., 18.I.1979 (AMS)

A cline exists from NE to SW across Isla Grande de la Tierra del Fuego, corresponding to both precipitation and vegetation gradients. *Staudingeri* phenotypes are increasingly frequent to the SW, but occur even at Río Grande in the extreme NE where populations are immense and variation very pronounced. Herrera and Field fail to note that Fuegian females are dimorphic in ground color: yellow, or white like the males. This is a genetic trait, as established by rearing.

Nominate *theodice* from Río Negro and *gymnodice/staudingeri* from Río Grande, T. del F., have been reared *ex ovo* and descriptions are in preparation. There are subspecific differences in the early stages.

Tatochila autodice Hübner (including *T. blanchardii* Butler)

Shapiro (1986a) demonstrated that *T. autodice* and *T. blanchardii blanchardii* intergrade in NW Patagonia, from Chos Malal, far N Neuquén, to C Chubut, mainly in the ecotone from the forested Patagonian Andes to bunchgrass — shrub steppe. Detailed records are presented there. The farthest S record for apparently pure *autodice* is Puerto Deseado, Santa Cruz, 1♂, 16.I.1967 (A. Willink) (ML). In 1989 I found *T. autodice* common in eastern Patagonia, viz. 1♀ Trelew, Chubut, 7.XII; 2♂ Las Plumas, Chubut, 7.XII; 3♂ Parada Uzcudún, Chubut, 7.XII; 1♀ El Tordillo, Chubut, 8.XII; 1♀ Pampa del Castillo, Chubut, 11.XII; 1♂ 2♀ Caleta Olivia, Santa Cruz, 9.XII; and 1♀ Fitz Roy, Santa Cruz, 9.XII. Both Caleta Olivia ♀ have an unusual yellow ground color but are otherwise typical. None shows any trace of *blanchardii* influence. Three of these localities represent tiny pockets of weedy Crucifers in extensive shrub-steppe, demonstrating the high dispersal capability of this species.

The farthest SE that *blanchardii* influence has been recognized is El Trébol, Chubut, 1♀, 12.II.1967 (A. Willink) (ML). Some intermediate phenotypes from Río Negro and Chubut are shown in Fig. 9. As noted in Shapiro (1986), the intergrading populations in the Lake District are unusually sparse. This is consistent with the now widely-recognized phenomenon of the "hybrid sink" (Barton and Hewitt 1985), although the intergrading population as Esquel is much larger; it is also in a drier climate and has a stronger *autodice* component. It should be noted that the usual host plants of the Lake District populations are native *Tropaeolum polyphyllum* rather than introduced weedy Crucifers, based on censuses done in 1988. At least some of the area occupied by these populations is mapped as recently (turn-of-the-century) deforested in Willis (1914).

The La Plata collection contains numerous apparently typical *blanchardii* from northwestern Patagonia, viz.: 1♂ Lago Lácar, Pucará, Neuquén, I.1958; 1♀ Lago Hermoso, Neuquén, I.1958; 1♀ Ruca Malen, Neuquén, undated; 1♀ Isla Victoria, Lago Nahuel Huapí, Río Negro, I.1960; 1♀ Quila Quina, Lago Lácar, Neuquén, I.1958; 2♀ San Martín de los Andes, Neuquén, I.1958; and 1♀ Lago Curahue, 950 m, Neuquén, I.1958. There is also one obvious ♂ intergrade, labeled "Río Negro," I.1936 (#2646).

On the basis of this rather extensive if mosaic intergradation I propose treating Herrera and Field's (1959) "*autodice* species group (Group B)" as a polytypic species, viz.:

Tatochila autodice Hübner 1818
Tatochila autodice blanchardii Butler 1881, new combination
Tatochila autodice ernestae Herrera 1954, new combination

Because nominate *autodice* and *ernestae* may be parapatric and altitudinally stratified in the Bolivian *yungas*, *autodice* may be a "ring species" (circular overlap, Mayr 1963, p. 507 *ff.*).

Tatochila mercedis Eschscholtz (including *T. sterodice* Staudinger, *T. fueguensis* Field, *T. macrodice* Staudinger, *T. arctodice* Staudinger, and *T. vanvolxemii* Capronnier)

This is the "*microdice* species group (Group C)" of Herrera and Field (1959). The incorrect use of the name *microdice* was corrected by Ackery (1975). Thereafter the name *sterodice* was used for a polytypic species embracing the taxa *fueguensis*, *macrodice* and *arctodice* — *mercedis* and *vanvolxemii* being treated as separate species. However, all the taxa of this group, from Colombia to northern Fuegia at least, are interfertile in the laboratory and intergrade through fairly sharply-defined hybrid zones wherever they come into contact afield (Shapiro 1979, 1984, 1986b and unpublished). The oldest name in the group is *mercedis* and all the other taxa may be considered subspecies of it. This action was initiated by Lamas and Pérez (1983) in listing *macrodice* as a subspecies of *mercedis*. "Group C," the "*sterodice* species-group" of my earlier papers, thus becomes:

Tatochila mercedis Eschscholtz 1821
Tatochila mercedis macrodice Staudinger 1898
Tatochila mercedis arctodice Staudinger 1898, new combination
Tatochila mercedis vanvolxemii Capronnier 1874, new combination
Tatochila mercedis sterodice Staudinger 1898, new combination
Tatochila mercedis fueguensis Field 1959, new combination

Because of intrinsic problems with the subspecies as a taxonomic category, and because one does not expect to find clear-cut taxonomic situations in groups as evolutionarily active as this one, a certain degree of arbitrariness seems inevitable in ranking the taxa. Cracraft

(1989), writing from one cladistic standpoint, denounces the ontological vacuity of polytypic species, a legacy of the Biological Species Concept, which he rejects. Nonetheless, the reproductive, genetic and geographic data available all appear to argue for polytypic-species status for this group, despite the morphological distinctness of some of its members; I accept the primacy of data over ideology.

The following, hitherto-unpublished data amplify the known Argentine distributions of these taxa and fill in gaps on previously-published maps (Figs. 10A, 11A).

Tatochila mercedis macrodice

Reported occurrences of this taxon in Argentina fall into three geographic regions; the *puna*, the Quichua District, and the Cuyo District.

(i) The *puna* of Jujuy and Salta

R. Eisele states (*in litt.*, 26.I.1978): "...according to Hayward...has been found as far S as Mendoza. In the last few years I have got a number of good series of this in Jujuy and Salta. All come from altitudes from 2450 to 4000 m and most common above 3000 m, at which altitude it is the most common *Tatochila*."

Some specific records:

2♂ Abra de Pives, Jujuy, 3900 m, 3.II.1969 (ML)
18♂ 13♀ Abra Pampa, Jujuy, 7.II.1984 (AMS)
14♂ 8♀ Esquinas Blancas, Jujuy, 7.II.1984 (AMS)
2♂ 31 km N Humahuaca, top Azul Pampa, Jujuy, 12.I.1978 (RE)
3♂ Abra Azul Pampa, Jujuy, 7.II.1984 (AMS)
6♂ Altos de Abra Muñano, Salta, 4165–4780 m, 21.I.1983 (AMS)

(ii) The Quichua District

This entity occurs in the *puna-jalca* alpine vegetation above the *yungas*. It is recorded in two geographic subdivisions:

(a) Salta highlands

3♂ Abra Molina, Salta, 22.I.1986 (AMS), 1♂ 2♀ 28.XI.1989 (AMS)
5♂ Cerro Zapallar, Salta, 22.I.1986 (AMS)
1♂ Valle Encantado, Salta, 3550 m, 14.XII.1976 (ML)

(b) The *Sierras Pampeanas* (Cumbres Calchaquíes, Sierra de Aconquija)

1♀ Cerro de la Mina, Depto. Tafí, Tucumán, IV.1933 (K. Hayward) (ML)
1♂ "Aconquija", 11.III.1917 (P. Jörgensen) (BM)
1♀ Esquina Grande, Catamarca, 1640 m, 30.XI.1915 (BM)
2♀ "Tucumán, 2000 m," III.1905 (J. Steinbach) (BM)
2♂ 1♀ Tafí del Valle, Tucumán, 2150 m, 30.XI.1977 (AMS)
3♂ Abra Infiernillo, Tucumán, 20.I.1986 (AMS), 2♂ 26.XI.1989 (AMS)

Specimens from the *Sierras Pampeanas* appear to average slightly smaller and more heavily marked than the others. Except for a genetically-determined ground-color polymorphism (white *vs.* yellow, white dominant — AMS, unpublished data) found in most populations, *macrodice* is extremely constant over its entire range in Peru, Bolivia, Chile and Argentina.

Like many butterflies of the *puna* and upper *yungas*, *T. m. macrodice* appears to migrate altitudinally with the season. It is present at lower altitudes in dry season than at other times, and disappears entirely from the vicinity of Tafí del Valle in January. However, as the 1989 data show, it emerges immediately in the highlands of both Salta and Tucumán with the onset of the rainy season in November, flying even before the vegetation has greened up. It thus must be 2- or more likely 3-brooded in the highlands, passing the dry season as a pupa, but no trace of diapause exists under laboratory conditions.

(iii) The Cuyo District

I have not found the documentation for the Hayward citation mentioned by Eisele. He did not include Mendoza for this entity in his (1950) *Catalogo Sinonímico*...but did in the posthumously-published 1973 catalog (p. 114). This reference also lists San Luis, a lowland Province whose highest point (in a pre-Andean range) is under 2000 m and which is unlikely to have any *macrodice* habitat at all. This suggests some kind of confusion existing in Hayward's mind late in his life concerning the identity of *macrodice*, and it is not hard to find evidence for this in museums. Herrera and Field (1959) record a specimen of *macrodice* from "Funes, Mendoza, January" which is the only precise locality ever published from Mendoza, but I have been unable to trace either the specimen or the locality. There is no "Funes" (or "Deán Funes") in Mendoza in available maps (Automóvil Club Argentino, sections 3 and 5, Carta Turística, 1969–72) or gazzetteers (US Department of Interior 1968).

ML contains a small female *vanvolxemii* from Potrerillos, Mza., 1500 m, 1947 (Hayward and Willink), misidentified as *macrodice*. La Plata has much more. Under *macrodice* (box 297) are 7♂ 4♀ from Potrerillos, X.1951. In addition, likewise identified as *macrodice* by Hayward, one finds a ♂ from Los Corrales, La Rioja, 1935 (lot #2643) (box 312) and a female without locality, "Junio 1925". All of these are *vanvolxemii*. Most are heavily marked, winter-spring forms. The *vanvolxemii* at Potrerillos may have some *mercedis* introgression and are undersized in summer. Also in La Plata are 1♂ 1♀ from Potrerillos (also X.1951) which were determined by Field as *vanvolxemii* but bear a handwritten label: "Opina Field que son intermedio de *microdice macrodice* o híbridos de éstos" ("Field opines that these are intermediate to *macrodice* or hybrids with it"). (See Porter and Shapiro 1990 for discussion of the Potrerillos population.) There is no current basis for recording *macrodice* in the Cuyo.

I have a single, highly unusual male from the highlands of San Juan which is in some ways intermediate between *macrodice* and *sterodice* or *mercedis*. Its data are: Arroyo de Agua Negra, 3300 m, 3.XI.1988 (AMS). The pattern is more or less midway between *macrodice* and *mercedis* (Fig. 12); the scales behind the eyes are white (as in *mercedis* or *sterodice*) rather than orange (as in *macrodice*); its compound eyes in life were gray-green, intermediate between the gray-blue of *sterodice* or *mercedis* and the bright chartreuse-green of *macrodice*, and unlike any other *Tatochila* I have examined alive in nature; and its genitalia, examined only externally, appeared to be arranged as in *sterodice* or *macrodice* rather than as in *mercedis*. I interpret this individual as possible evidence for a transition from *macrodice* to *mercedis* in the very-poorly-collected zone of transition from the Quichua to the Cuyo District.

Given the amount of collecting done in the vicinity of the Paso Bermejo (Las Cuevas, Punta de Vacas, Puente del Inca) in the past century, if *macrodice* occurs in that easily accessible locality in the *cordillera* of Mendoza it must be either at very low density or at altitudes above 4200 m, which are less well-known. I did not find it there (up to 4350 m) in six days in XI–XII. 1989.

Tatochila mercedis vanvolxemii

The winter form of this widespread and common entity shows the complete *sterodice* pattern in the male. As only reared (experimental) examples have been figured heretofore, and then not in systematic or biogeographic works, I provide (Fig. 13) wild-collected ones from the "core" range where introgression from other subspecies is highly unlikely.

The NW limits of *vanvolxemii* have been in question. It has often been cited from "Tucumán," which is usually (and often wrongly) interpreted as referring to the capital, San Miguel de Tucumán, where it definitely does *not* occur (and has not in historic times). The only definite records I have from the Province of Tucumán are from Amaichá del Valle: 4♂ 3♀, 4.II.1984 and 1♀, 26.XI.1989 (all AMS). Amaichá, on the dry side below Abra Infiernillo en route to the Valles Calchaquíes, is a high-desert locality. More or less similar habitat occurs up the Valles Calchaquíes (Río Santa María drainage, the N-most extent of the *monte*) as far as the vicinity of Cachi, Salta where I have collected only *T. autodice* and *Ascia monuste automate* Burmeister. Thus we may infer that *vanvolxemii* follows the *monte* to near its N limit but does not extend into the *prepuna*. If *T. m. vanvolxemii* is a permanent resident at Amaichá it is spatially very close to *T. m. macrodice*, though altitudinally and ecologically segregated. Our samples from Amaichá are very small to detect introgression from *macrodice*. Two of the females are unusually heavily-marked, and one is the darkest *vanvolxemii* I have seen. The XI.1989 female is old and worn but vaguely suggestive of *macrodice* influence. It does seem certain that there is no extensive intergradation, such as occurs farther south in this polytypic species.

Populations of apparently pure *vanvolxemii* occur at low-elevation, desertic sites quite close to the zone of intergradation with *sterodice* and *mercedis* in NW Patagonia. Examples are:

2♂ Covunco, 820 m, Neuquén, 12.XI.1966 (MG)
2♂ 1♀ Estancia Corral de Piedra, Collón Curá, Neuquén, 650 m, 3.XII.1969 (MG)
1♂ Las Lajas, Neuquén, 730 m, 15.I.1980 (MG)

The Collón Curá series includes both extreme winter forms and intermediates to the summer form. A similarly mixed series was taken at Zapala, Neuquén, 9–11.XI.1988 (AMS). This is also a pure population. The occurrence of winter forms as late as early December at low altitude is fairly unusual; they normally occur only in the first brood. Control of the polyphenism is discussed in Shapiro (1980a).

Typical *vanvolxemii* (averaging small) are abundant in eastern Patagonia as far south as Trelew (18♂ 5♀, 7.XII.1989), Las Plumas (43°43′S, 67°15′W, 11♂ 6♀, 7.XII.1989), and Parada Uzcudún (44°13′S, 66°09′W, 17♂ 17♀, 7.XII.1989) (all Chubut, all AMS). At Trelew oviposition was observed on *Cardaria draba* (L.) Desv. (Cruciferae), usually a disfavored Pierid host.

Records of *T. m. vanvolxemii* from "Buenos Aires" have always been ambiguous due to confusion of the city and the Province. On 23.XI.1989 it was common in the city (Costanera Sur, Avenida de los Italianos, Zona Portuaria, vacant lots in La Boca), the first time I have seen it there.

Hybrid Zones involving *T. m. vanvolxemii*

2♂ 13♀Loncopué, Neuquén, 8.XI.1988 (AMS)

This remarkable series marks a new N limit (38°04′S) for the zone of intergradation, or hybrid zone, between *vanvolxemii* and other entities. Although very close to Aluminé (39°13′, 70°57′W), this population is phenotypically very different. The Aluminé population shows no significant *vanvolxemii* component, while that at Loncopué is mostly *vanvolxemii* (by phenotype). The females are most like *vanvolxemii*, with variable *sterodice* influence. The two males differ astonishingly from each other: one resembles the putative *sterodice-vanvolxemii* hybrid from Bariloche figured by Shapiro, 1980a (which in turn resembles series of this cross, reared in the laboratory under summer photoperiod/temperature regimes); the other resembles a winter form of *vanvolxemii* below and a *sterodice-mercedis* intergrade with strong sagittate pattern above. All of these (Fig. 14) were taken flying together in one pasture. The host plant is *Lepidium* sp. (Cruciferae).

Loncopué is, as noted above, the N-most locality known for *T. theodice* in Argentina. It is also the N-most locality for the skipper *Hylephila signata* Butler and the third most N for *Colias vauthierii* Guérin, discussed later. Both of these are typical Patagonian *mallin* species which rarefy progressively as one moves N into the transition to the *cuyo*.

22♂ 11♀ Barrio Próspero Palazzo, Comodoro Rivadavia, Chubut, 19.XI.1988 (AMS) Several previous collections from Comodoro Rivadavia (San Jorge District) (45°52′S, 67°30′W) were made in high summer and had produced the erroneous impression that the population there was pure *vanvolxemii*. As noted above, summer *vanvolxemii* lose most or all of the black pattern in the male, and this is the summer phenotype at Comodoro. This large series of the first (ex diapause), spring generation — in which the pattern is fully expressed — reveals a strong apparent admixture of *sterodice* genes (most apparent in the dotted DFW pattern, which is almost never seen in *vanvolxemii* in its "core" range far from hybrid zones). A few of these Comodoro males would unhesitatingly receive *sterodice* labels if considered out of context.

In 1989 a systematic attempt was made to map the distribution of intergrading populations in eastern Patagonia. Populations very similar to that at Comodoro were found at: El Tordillo (45°53′S, 67°57′W, 6♂ 5♀, 8.XII); Pampa del Castillo (45°48′S, 68°65′W, 13♂ 7♀, 11.XII), both Chubut; Caleta Olivia (46°26′S, 67°32′W, 9♂ 6♀, 9.XII) and Fitz Roy (47°02′S, 67°15′W, 25♂ 7♀, 9.XII), both Santa Cruz (all AMS).

The seasonal polyphenism of *vanvolxemii* is expressed in the San Jorge region superimposed on a mixed genetic background. This phenomenon, as noted above, is best detected in the spring brood and it remains to be seen if these populations differ among themselves in the strength of the polyphenism. The occurrence of the intermediates here is consistent with the anomalous climatic and vegetational character of the San Jorge District, reflected also in the abundance of *T. a. autodice*, *Colias lesbia*, and other species much farther south than they occur in the interior. Between Fitz Roy and Comandante Luís Piedrabuena all trace of *vanvolxemii* phenotype disappears. Although I have visited both San Julián (49°18′S, 67°43′W) and Puerto Deseado (47°45′S, 65°54′W), I have collected no *Tatochila* due to bad weather. ML, however, contains a Puerto Deseado male which if anything shows a transition from *sterodice* to *fueguensis* phenotype, certainly nothing of *vanvolxemii*. MLP contains 3 San Julián specimens which appear to be pure *sterodice*. All trace of *vanvolxemii* also disappears between Pampa del Castillo and Sarmiento (45°36′S, 69°05′W).

Fig. 15 demonstrates the variation in the first brood at Comodoro.

MLP also contains a ♀ from San Martín de los Andes, Neuquén, 2.I.1958, which resembles closely a lab F_1 hybrid between *mercedis* and *vanvolxemii* (not involving *sterodice*).

Tatochila mercedis sterodice

Populations of *T. m. sterodice* are extremely variable even when not plainly involved in intergradation with other taxa; indeed, there are few characters which are sufficiently constant throughout its range as to be diagnostic. Thus, singletons or short series are of limited use in characterizing geographic patterns of variation. The range of variation is, however, broader still in zones of contact with other taxa, and numerous novel phenotypes not seen elsewhere occur there. When in contact with nominate *mercedis* in NW Patagonia, *sterodice* displays lability in genitalic morphology as well as in wing pattern. Elsewhere, its genitalia are constant (Porter and Shapiro 1989).

The following short series all appear to fall within the "normal variation" displayed by "pure *sterodice*." The Valle Lago Blanco series is especially variable, and one specimen from there (reported below) appears to be a hybrid with *mercedis*. The neotype of *sterodice* designated by Ackery (1975) is singularly unfortunate in being at the heavily-marked end of the "normal variation" spectrum. Moreover, the entire type-series of *sterodice* came from within the zone of intergradation to *fueguensis*, in the far S of the range of *sterodice*. The synonym *allodice* Bryk, from LLau-LLau (near Bariloche) would make better geographic sense!

1♂ Estancia Huechahue, Neuquén, 14.XI.1988 (AMS)
2♂ Chapelco, 1750 m, Neuquén, 20.II.1973 (MG)
1♀ Arroyo Chapelco Grande, Neuquén, 900 m, 15.XII.1970 (MG)
1♂ Cordón Chapelco, Portezuelo Trahunco, 1750 m, Neuquén, 27.XII.1978 (MG)
3♂ Refugio Graeff, Parque Nacional Lanín, Neuquén, 1750 m, 12.III.1980 (MG)
1♂ Lago La Kika, Neuquén, 1750 m, 24.I.1979 (MG)
1♂ Quila Quina, Lago Lácar, Neuquén, I.1958 (MLP)
4♂ Pulmarí, Río Alumine, Neuquén, 4500′, Feb.1902 (H. J. Elwes) (BM)
1♂ Bariloche, Río Negro, III.1948 (Williamson & Martínez Fontes) (MR)
1♂ Parque Nacional Nahuel Huapí, Dec. 1912 (BM)
1♂ Puerto Blest, Lago Nahuel Huapí, Río Negro, 770 m, loc. #8, 1.III.1979 (DE)
1♂ Cañada León, Chubut, no date (MLP)
1♂ Alto Río Senguerr, Chubut, 18.XI.1988 (AMS)
1♂ Colonia Sarmiento, Chubut, 600 m, loc. #46, 15.II.1979 (DE)
4♂ Tecka, Gobernador Costa, Chubut, 600 m, loc. #23, 7.I.1979 (DE)
1♀ Tecka, Chubut, 3000′, Jan.–Feb. 1920 (BM)
2♂ 1♀ Valle Lago Blanco, Chubut, "Thursby 1904–26" (BM)
1♂ 1♀ Glen Kross, Santa Cruz, II.1938 (MLP)
1♂ Lago Argentino, Península Magallanes, Santa Cruz, loc. #28, 1.II.1979 (DE)

3♂ San Julián, Santa Cruz, no date (MLP)
1♂ Cte. Luís Piedrabuena, Santa Cruz, 20.XI.1988 (AMS)
1♂ Lago Onelli, Santa Cruz, II.1953 (MLP)

Tatochila mercedis fueguensis

Herrera and Field (1959, p. 488) state that this is "probably most distinct" among the subspecies of "*microdice*" (=*sterodice*). Once again this impression was an artifact of lack of far-S material. Such material, once assembled, demonstrates an unequivocal and relatively even cline from *sterodice* to *fueguensis* phenotypes. The following records represent elements of that cline. Although some individuals are "typical" *fueguensis*, none of the longer series is, and some of the La Esperanza material *from the mainland* is phenotypically indistinguishable from topotypical *fueguensis* (Fig. 16).

2♂ 4♀ La Esperanza, Santa Cruz, 130 KM NW Río Gallegos, loc. #30, 15.I.1979 (DE)
1♂ Perito Moreno, Río Fénix, Santa Cruz, XII.1982 (J. Carreras) (MR)
3♂ Estancia La Cristina, near Lago Argentino, Santa Cruz, 8.II.1953 (A. Willink) (ML)
1♂ Puerto Deseado, Santa Cruz, 16.I.1967 (A. Willink) (ML)
1♀ Cantería Masci, Río Gallegos, Santa Cruz, 22.XI.1988 (AMS)
3♂ Río Gallegos, Santa Cruz, 10.II.1979, loc. #31 (DE)
3♂ 6♀ Río Gallegos, Santa Cruz, 23.I.1979 (AMS)
2♂ Lago Fagnano, Tierra del Fuego, 100 m, loc. #33, 19.I.1979 (DE)

Tatochila mercedis mercedis

The location of the zone of intergradation between *sterodice* and *mercedis* has been documented previously (Shapiro, *loc. cit.*) but the following hitherto unpublished records are of interest because they fill in gaps, or because they demonstrate that hybridization has been in progress for at least several decades.

(a) Apparent hybrids or intergrades
1♂ Cerro Malo, 1700 m, Neuquén, 15.II.1954 (S. Schajovskoy) (MR)
1♂ 1♀ San Martín de los Andes, Neuquén, XII.1952 (S. Schajovskoy) (MR)
1♂ Pucará, Neuquén, 13.III.1960 (S. Schajovskoy) (MR)
1♀ Pucará, Neuquén, 19.III.1960 (S. Schajovskoy) (MR)
1♂ Refugio Graeff, Parque Nacional Lanín, Neuquén, 1750 m, 2.I.1980 (MG)
1♂ San Martín de los Andes, Neuquén, 5.XI.1979 (MG)
1♀ San Martín de los Andes, Neuquén, 640 m, 6.I.1978 (MG)
1♀ San Martín de los Andes, Neuquén, extreme winter form, 15.XI.1969 (MG)
1♂ San Martín de los Andes, Neuquén, I.1958 (MLP)
1♀ San Martín de los Andes, Neuquén, 1.II.1939 (MLP)

1♂ 1♀ Lago Lácar, Pucará, Neuquén, 750 m, loc. #9, 1.XII.1978 (DE)
3♂ 1♀ Quila Quina, Lago Lácar, Neuquén, I.1958 (MLP)
1♂ Aluminé, Neuquén, 1200 m, loc. #57, 14.III.1979 (DE)
1♂ 2♀ Estancia Aschieri, below Primeros Pinos, Neuquén, 1130 m, 9.XI.1988 (AMS)
1♂ El Bolsón, Lago Puelo, Río Negro, Loc. #13, 26.II.1979 (DE)
1♂ "Chile (*sic*), El Bolsón," no date (A. Kovacs) (BM)
1♂ Valle Lago Blanco, Chubut, "1904–26", #10316 (BM)
(b) Indistinguishable from Chilean *mercedis*
1♂ Pucará, Neuquén, 22.I.1958 (S. Schajovskoy) (MR)
1♂ 1♀ Pucará, Neuquén, 15.II.1956 (S. Schajovskoy) (MR)
1♂ Caviahue, Neuquén, 1500 m, 25.II.1962 (S. Schajovskoy) (MR)
1♂ Lago Lácar, Pucará, Neuquén, 750 m, loc. #9, 1.XII.1978 (DE)
1♀ Quila Quina, Lago Lácar, Neuquén, I.1958 (MLP)
1♂ 1♀ San Martín de los Andes, Neuquén, II.1939 (MLP)
1♂ San Martín de los Andes, Neuquén, I.1958 (MLP)
1♀ San Martín de los Andes, Neuquén, III.1952 (S. Schajovskoy) (MLP)
(c) Miscellaneous

The following specimen appears to be a complex hybrid involving *vanvolxemii*, *mercedis* and *sterodice*; it matches certain laboratory-reared hybrids of that composition almost exactly:
1♀ Pulmarí, Río Aluminé, Neuquén, 925 m, 27.II.1978 (MG)

Interspecies Hybrids

The following may be a unique hybrid of *T. a. autodice* and *T. m. vanvolxemii*, showing a mix of characters of both. Both putative parents occur at the site. They are in fact sympatric over nearly half the country, so hybrids must be extremely rare since this is the only suspected one yet found. This hybrid has not been produced in the laboratory.
1♂ Las Lajas, Neuquén, 730 m, 15.I.1980 (MG)

"Group D" *Tatochila* (the "*orthodice* group")

This is a heterogeneous and possibly not monophyletic group. Ackery's (1975) work has increased our knowledge of the central-Andean members of this group, but species limits remain very poorly defined and some of his assignments of subspecies to species may be incorrect. The entire group may be Legume rather than Crucifer specialists. In Argentina they extend only barely to Córdoba; most species are found in the *Yungas* and Quichua District.

Tatochila inversa Hayward (Fig. 17A, B, Plate IV)

Herrera and Field (1959) figured as the male of this species something from the Department of Cusco, Peru. Whether this is really *inversa* remains uncertain, but true *inversa* males are now available from various localities in northwestern Argentina. They differ phenotypically among populations and perhaps between broods as well (Fig. 17, from the *puna*; Pl. IV, from the *Sierras Pampeanas*) but differ from Herrera and Field's specimen in a number of details. The species is not rare on summits within the *puna*. The type locality — Quebrada Carapunco — is near Abra Infiernillo in the *Sierras Pampeanas* of Tucumán. Animals from these ranges average larger than those from elsewhere. If a subspecies name is ultimately necessary it would apply to the smaller phenotype from Salta and Jujuy.

Eisele writes (*in litt.*, 26.I.1978): "Just got my first female (*inversa*) from the mountains in Salta. I had previously got a number of males from Jujuy." One of these is figured: Huacalera, N end Cerro Amarillo, Jujuy, 3250 m, 4.I.1980 (RE). Other records: Abra Infiernillo area, Tucumán, 1♂, 26.XI.89, 3♀, 20.I.1986 (AMS); 1♀ Cerro Zapallar, 3720 m, Salta, 22.I.1986 (AMS); 1♀ Abra Azul Pampa, Jujuy, 23.I.1986 (AMS).

The Infiernillo records suggest that this species may be multiple-brooded. The 26.XI.89 male was taken at the very beginning of the rains, before the vegetation had resumed growth.

Tatochila orthodice Weymer

This is a well-known and common species of N Argentina and adjacent Bolivia, essentially restricted to the *yungas*. Most records are low-to-mid montane. It is not generally recognized as a component of the high-Andean fauna but in fact occurs there seasonally in January, flying with *T. m. macrodice*, *T. inversa*, *T. distincta*, etc. This altitudinal migration occurs at the *yungas-puna* and *yungas*-Quichua District interfaces, including the *Sierras Pampeanas*. Some high-altitude records: 1♀ Abra Infiernillo, summit near 3800 m, 20.I.1986 (AMS); 2♂ 1♀ Valle Encantado, 9725′, Salta, 22.I.1986 (AMS); 2♀ Cerro Zapallar, 3700 m, Salta, 22.I.1986 (AMS). At the time these were collected, no *orthodice* were flying in the foothills just above San Miguel de Tucumán, where the species is typically abundant in spring (Anta Muerta, 26.XI.1977; El Siambón and Sala de San Javier, 26.XI.1977, all AMS). I have a mid-elevation record seasonally inbetween these (Tafí del Valle, 2200 m, 26.XII.1977, AMS).

This species was common at La Viña, Catamarca, 29.XI.1989 (AMS).

Tatochila stigmadice Staudinger

Also best-known as a foothill *yungas* species, *T. stigmadice* occurs occasionally in the high country in summer and also as low as the city of San Miguel de Tucumán. My extreme records are: 1♀ Cerro Zapallar, 3600 m, Salta, 22.I.1986 (AMS); 2♂ Barrio Fray Usquiu, S.M. de Tucumán, 450 m, 28.XI.1977 (AMS); I♂ San Miguel de Tucumán (centro, along R.R. track), 29.XI.1989 (AMS). It was also flying at San Javier, Tucumán and La Viña, Catamarca the same day.

The southernmost record of this species is apparently an unusual, white female from Yacanto, Córdoba, no date (Breyer) (MLP). The Sierras de Córdoba have a dilute *yungas* element.

"Group E" *Tatochila* (the "*xanthodice* group")

Although this group contains only two species, they are united only by genitalic morphology. Their wing patterns, biogeography, and host plants are different enough to raise serious doubts as to their true affinity, and the morphology of the early stages is also somewhat equivocal.

Tatochila distincta Jörgensen (Fig. 17C, D)

The La Plata collection contains two Jörgensen specimens: ♂, Cerro Ensenada (Catamarca), 22.II.1915 (#2651) and ♀, Cerro Negro, same date (no number). These were selected in 1971 by L.E. Peña as "hololectotipo" and "allolectotipo" respectively, and so labeled. Both are small and dark.

Not uncommon between 3000–4000 m in dissected *puna*, and in the Quichua District including the *Sierras Pampeanas*, flying with *T. inversa* and *T. m. macrodice*. The life-history of this species has been published (Shapiro 1986d). It is apparently an *Astragalus*-feeder (Leguminosae) in nature, but can be reared on Crucifers. There are phenotypic differences between the Salta and Jujuy populations on one hand and the (topotypical) material from the *Sierras Pampeanas* (Cumbres Calchaquíes — Aconquija), which may ultimately justify naming subspecies within Argentina. Sexual dimorphism is somewhat reduced in this species.

2♂ 20 km N Humahuaca, Salta, 3700 m, 12.I.1978 (RE)
8♂ 3♀ Tres Cruces, Jujuy, 3800 m, 23.I.1986 (AMS)
1♂ 1♀ Abra Infiernillo, Tucumán, 20.I.1986 (AMS)
2♀ Cerro Zapallar, Salta, 3720 m, 22.I.1986 (AMS)

Genus *Hypsochila* Ureta (Figs. 18, 19; ranges 10B, 11B)

In early stages as well as adults, one group of species of *Hypsochila* appears to be the sister-group of the *Tatochila mercedis* and *autodice* (Crucifer-feeding) complexes. Unfortunately, the genus *Hypsochila* itself is in some disarray despite work by Ureta (1955, 1963) and a revision by Field and Herrera (1977). The latter was regarded by its authors as very preliminary, and was based largely on Herrera's Chilean material. The species limits were poorly defined, and the authors went so far as to state (p. 5): "Five of the six species. . . are very closely related and could be considered subspecies of a single widely distributed species. However. . . two of these species are known to fly at the same time in at least two of the same localities..." The data reported here demonstrate that Field and Herrera were wise in continuing to treat these taxa as species, though tantalizing ambiguities remain. The Argentine species appear to fall into two groups, based on both adult and immature characters. Because the type-species is *H. wagenknechti* Ureta, the group to which it belongs (comprising in addition the taxa *sulfurodice* Ureta and *galactodice* Ureta) will retain the generic name, should the genus be divided as seems likely. This group has close affinities to *Tatochila* as noted above. The other group, comprising the taxa *argyrodice* Staudinger, *microdice* Blanchard and *huemul* Peña, has many unusual derived character states and is farther removed from *Tatochila*. All of its taxa are austral in distribution. No name is currently available for the group, should it be formally raised to subgeneric or generic status.

Hypsochila argyrodice **(Fig. 18C)**

1♂ Cabo Peñas, Depto. Río Grande, Tierra del Fuego, 17.XII.1983 (ML)
1♂ Fitz Roy, Santa Cruz, loc. #26, 11.II.1979 (DE)

Hypsochila microdice **(Fig. 18G, H)**

37♂ 11♀ Río Grande, Tierra del Fuego, 25.XI.1988 (AMS)
1♂ Estancia María Cristina, Route 3, Tierra del Fuego, 27.XI.1988 (AMS)
1♂ 1♀ Foot of Glaciar Martial, Cordón Martial above Ushuaia, T. del F., 29–30.XI.1988 (AMS)

These combined records demonstrate that the ranges of the two southernmost *Hypsochila* interdigitate and they cannot be conspecific. The Danish Expedition *argyrodice* from Fitz Roy appears to be the first mainland specimen with a precise locality. Breyer (1939) never saw it at all, even a specimen, but cites "Ushuaia, Röber." Hayward (1950, p. 92) records "Chubut" without data. I searched unsuccessfully for it in marginal weather at Fitz Roy on 20.XI.1988. *H. microdice* is abundant at Río Grande and its life-history is in preparation. The phenotype is quite variable, but not easily confused with anything else in the region. The two Cordón Martial specimens are large, especially the male, but still smaller than *argyrodice*. *Microdice* is a Legume-feeder and given the very close morphological affinities, the others are likely to be as well. I have no new data to report on *H. huemul*.

Hypsochila galactodice **(Fig. 18D, E; 19C, F, G, H)**

1♀ Río Agrio, Neuquén, 10.IV.1932 (MLP)
2♂ Huacalera, N end Cerro Amarillo, 3250 m, Jujuy, 4.I.1980 (RE) (*)
1♂ Cordón del Viento, Neuquén, 3000 m, 28.I.1985 (AMS) (*)
2♀ Lago Meliquina, Neuquén, loc. #10, 12.XI.1979 (DE)

1♂ 1♀ Aluminé, Neuquén, 15–16.I.1981 (AMS)
1♂ Junín de los Andes, Neuquén, 13.XI.1988 (AMS)
1♀ Loncopué, Neuquén, 8.XI.1988 (AMS) (*)
1♂ 6♀ San Carlos de Bariloche, Río Negro, 15.XI.1988 (AMS)
13♂ 4♀ Esquel, Chubut, 17.XI.1988 (AMS)
(plus reared diapaused and non-diapaused material from Bariloche and Esquel)

Hypsochila wagenknechti wagenknechti **(Figs. 18I, 19A, D)**

6♂ 2♀ Las Cuevas, Mendoza, 31.X–1.XI.1988 (AMS)
21♂ 11♀ Arroyo de Agua Negra, above 3200 m, San Juan, 3.XI.1988 (AMS)

Hypsochila wagenknechti wagenknechti **"spring form"**

1♂ 1♀ Arroyo Chapelco Grande, 900 m, Neuquén, 15.XII.1979 (MG)
1♂ Chapelco, Neuquén, 1700 m, 24.II.1952 (S. Schajovskoy) (ML)

Hypsochila wagenknechti sulfurodice **(Fig. 18A, B, F)**

1♂ Huacalera, N end Cerro Amarillo, 3250 m, Jujuy, 4.I.1980 (RE)
3♂ Altos de Abra Muñano, 4165–4780 m, Salta, 21.I.1983 (AMS)
8♂ Tres Cruces, 3800 m, Jujuy, 7.II.1984 (AMS)

This group of taxa is so difficult that some critical determinations are provisional (marked *). The life-histories of *H. w. wagenknechti* and *H. galactodice* are fully known (Courtney and Shapiro 1986a, b; Shapiro, in preparation). They differ about as much as the adults: *wagenknechti* feeds in nature on Crucifers, *galactodice* on *Tropaeolum*. Brown (1987, p. 102) maps these two species as either allopatric or parapatric at roughly 32°S. Field and Herrera have *galactodice* only from Epulafquén, Neuquén on the Argentine side and *wagenknechti* only from Las Cuevas and the directly adjacent Quebrada de los Horcones, Mendoza — widely-separated localities, falling in the Western Patagonian District and the Cuyo District respectively. The Loncopué female and the male from Cordón del Viento, Neuquén are both virtually undeterminable, and both are geographically feasible as zones of primary (not secondary?) intergradation if these two taxa are biologically conspecific. To complicate matters, a second female *Hypsochila* taken the same day at Loncopué is quite different and does not agree with any described taxon.

The pair of apparent *galactodice* from Cerro Amarillo, Jujuy is extremely problematical. Although matching the description of *galactodice*, they differ from Patagonian specimens in exactly the same ways *sulfurodice* differs from nominate *wagenknechti*. If *H. galactodice* actually occurs some 2000 km N of its previously-known range, in a different biome and sympatrically with a subspecies of *wagenknechti*, there can be no question of conspecificity with that species. However, the series is too short to rule out sampling error disguising continuous population variation at Cerro Amarillo, from a usual *sulfurodice* to a *galactodice*-like phenotype. My long series of *wagenknechti wagenknechti* from Mendoza and San Juan includes individuals which approach *galactodice* in phenotype, underscoring the variability of these animals and the potential unreliability of small samples. Unfortunately, females are rarely encountered and males are concentrated on relatively inaccessible hilltops, where they are difficult to catch. In the absence of *any* reliable, diagnostic morphological character this problem is insoluble at this time. Absolutely no tendency to resemble *galactodice* has been seen in any other *sulfurodice* (i.e. from localities other than Cerro Amarillo).

In the Cordón Chapelco near San Martín de los Andes a small, very dark form of (?)*wagenknechti* occurs in which the dorsal apical markings tend to fuse; the reflective gloss at the base of the wings is more pronounced; and the VHW pattern is extremely heavy. The pattern is vaguely suggestive of the next species. I am treating these as spring forms of *wagenknechti* because I have very similar specimens from Chile: Cumbres de La Parva, Prov. Santiago, 24.XI.1982 and Los Libertadores, Prov. Los Andes, 3900 m, 27–28.I.1983 (all AMS), taken right at melting snow-line in an area (just across the Paso Bermejo from Las Cuevas) where no other taxon is at issue. However, seemingly typical *galactodice* occurs at Junín de los Andes (first brood, XI.13), quite close to but lower than the Cordón Chapelco.

Near Las Leñas in southern Mendoza, 3♂ *Hypsochila* were collected on an altitudinal transect up Cerro de los Fosiles, 3.XII.1989: a typical *galactodice* at 2100 m, an intermediate specimen at about 3000 m and a typical *wagenknechti* at 3300 m. All are figured on Plate IV. Again, this suggests altitudinal stratification and intergradation (but the sample size is very small). Strikingly, the two higher specimens were hilltopping while the low-altitude one was visiting a dandelion on a *vega*, behaving much as a *galactodice* "should."

Problematic specimens of this group of taxa, including a striking aberration of *wagenknechti*, are shown in Figs. 18–19.

Hypsochila penai Ureta

So far known only from Chile. A ♂ in ML is labeled "Alto de Puripica, 4600 m." The country is not given. This locality is in Chile (22°30′S, 68°07′W) quite close to the Argentine border.

Genus *Phulia* Herrich-Schaeffer (Fig. 20; ranges 10C, 11C)

This is a classically high-Andean genus, restricted to *puna* and *altiplano* from C Peru through Bolivia to NE Chile and NW Argentina. All the Argentine populations known are treated by Field and Herrera (1977) under the name *P. nymphula* Blanchard. Genetically and ecologically these populations are somewhat diversified. Life-history and electrophoretic data will be published (Shapiro, Courtney, Descimon & Geiger, in preparation).

In Argentina "*P. nymphula*" is distributed in four geographic regions. Rather than multiply names, I present representative data and discuss the status of available names potentially applicable to these populations.

(i) The *puna* of Jujuy and Salta

26♂ 13♀ Tres Cruces, Esquinas Blancas, Jujuy, 7.II.1984 (AMS), 23.I.1986 (AMS)
2♂ Abra de Pives, 4200 m, Jujuy, 29.I.1969 (ML)
1♂ near Turilari, Jujuy, 4000 m, 5.IX.1968 (ML)
1♀ Rosario de Coyahuayma, Salta, 4400 m, 11.IX.1968 (ML)
1♂ Río Cincel, Jujuy, 3800 m, 3.IX.1968 (ML)

Plate I. Pierid habitats in montane northwestern Argentina. A, view of *puna* dominated by *tola*, looking N from a summit near Abra Muñano, Salta; habitat of *Hypsochila wagenknechti sulfurodice*. ii.1983. B, Dissected *puna* at the head of the Quebrada de Humahuaca, Jujuy, near Abra Azul Pampa. Habitat of *H. w. sulfurodice*, *Tatochila distincta*, *T. mercedis macrodice*, *Phulia nymphula*, and *Colias blameyi*. ii.1985. C, *Yungas* in Salta, below Valle Encantado, showing deeply dissected topography. Habitat of *Tatochila orthodice* and *stigmadice* and *Teriocolias riojana*. i.1986. D, Valle Encantado, Salta, in the uppermost *yungas*, at the height of wet season; *Colias blameyi*, *Tatochila orthodice*, *T. stigmadice*, *Teriocolias riojana*. i.1986. E, Rocky summit in the Cumbres Calchaquíes, Tucumán (quichuan vegetation with large *Azorella* in foreground). Habitat of *Tatochila inversa*, *distincta*, *mercedis macrodice*, and *Colias blameyi*. i.1986. F, Dry subalpine shrub-steppe above Amaichá del Valle, Tucumán, looking toward the Valles Calchaquíes. This belt forms the apparent barrier between *Tatochila mercedis macrodice* above and *T. m. vanvolxemii* below. i.1986. All photos by AMS.

Plate II. Pierid habitats in montane west-central Argentina. A, *prepuna* with columnar cacti near Cachi, Salta. No endemic Pierid fauna, but *Tatochila autodice* and (seasonally) *Ascia monuste automate* common. i.1986. B, Riparian vegetation in wet season in the *monte*, Valles Calchaquíes between Fuerte Quemado and Cachi. *Tatochila mercedis vanvolxemii* occurs in similar vegetation farther S but is not known N of Amaichá del Valle at this time. i.1986. C, Precordillera near Potrerillos, Mendoza. *T. m. vanvolxemii* with possible introgression from *T. m. mercedis* are abundant here. x.1988. D, *Vega* at the head of the Arroyo de Agua Negra, San Juan, near the Chilean border. The only known locality for *Colias flaveola* in Argentina. Nearby occur *Hypsochila w. wagenknechti*, *Phulia nymphula* and other characteristic cordilleran taxa. xi.1988. E, Sparse alpine steppe in the Aconcagua Provincial Park, Mendoza, in early spring; *Phulia nymphula* very abundant. xi.1988. F, Rockslides among the summits overlooking the Paso Bermejo, Mendoza. *Hypsochila w. wagenknechti* abundant. xi.1988. All photos by AMS.

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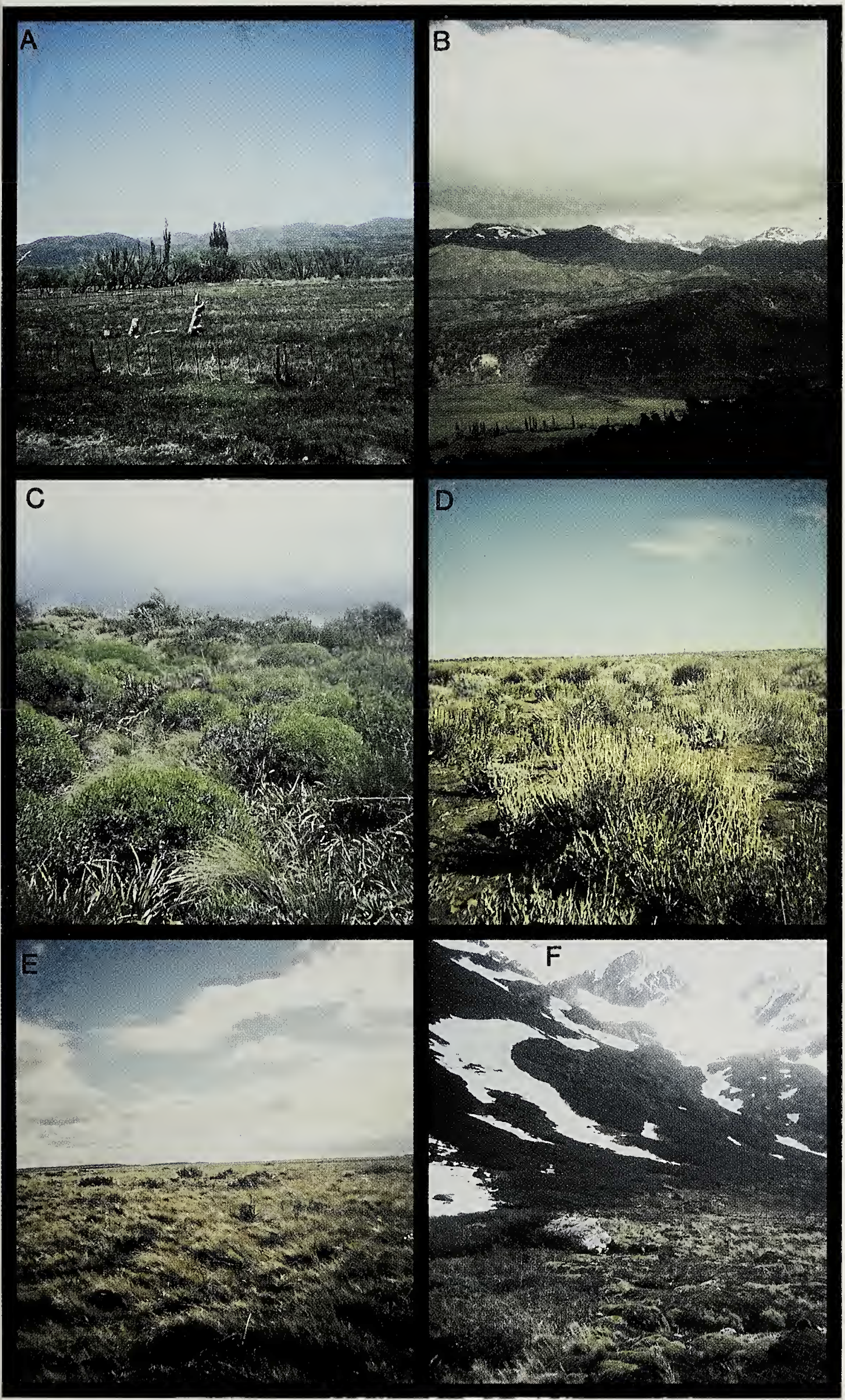
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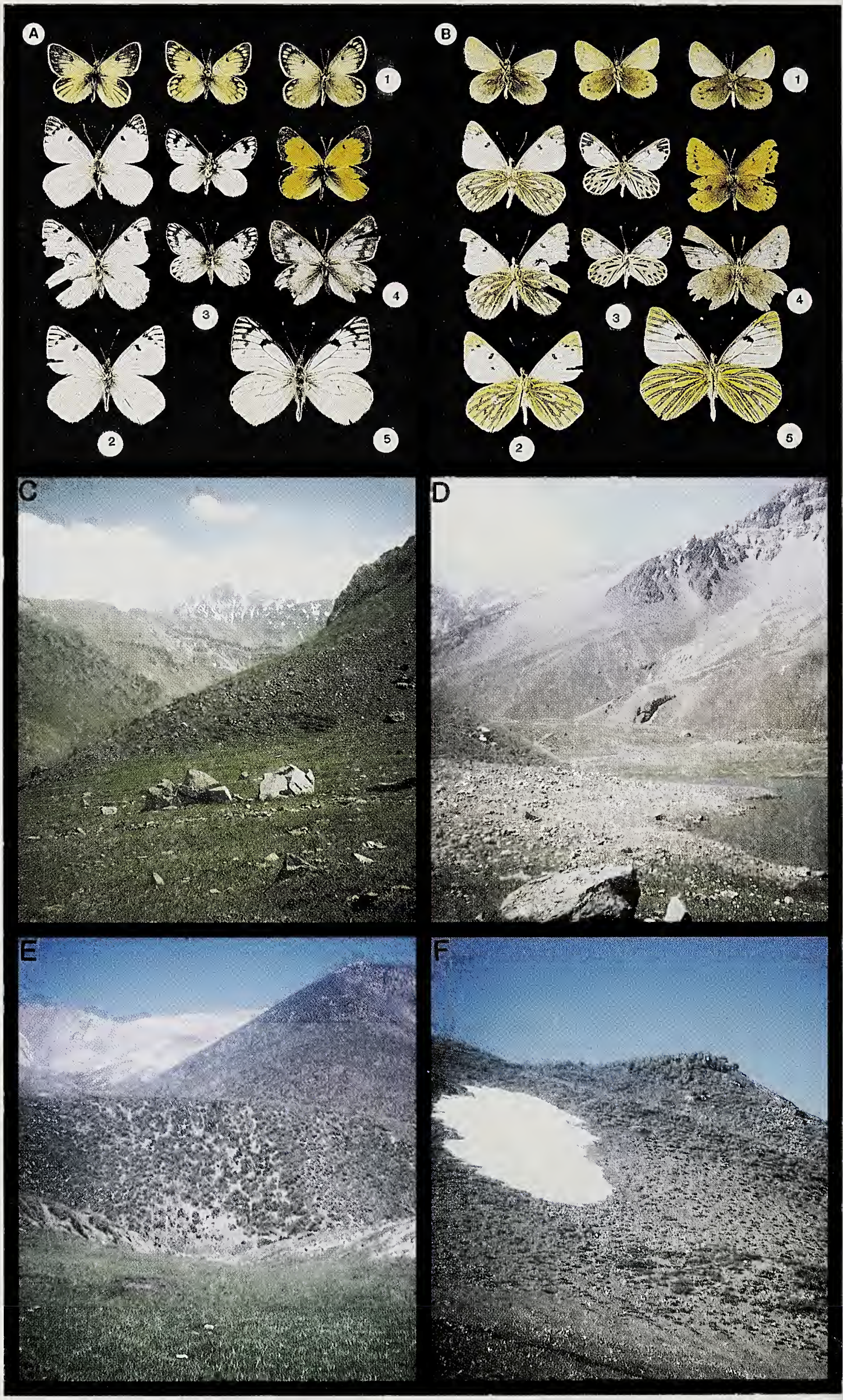
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Plate III. Pierid habitats in southern Argentina. A, partially inundated *mallines* at Loncopué, Neuquén, site of a hybrid *Tatochila mercedis sterodice* X *vanvolxemii* population. Also occurring here are *T. theodice, Hypsochila galactodice, Colias vauthieri,* and various other Patagonian taxa near or at their N limits. xi.1988. B, Mosaic of *Nothofagus* forest, subalpine steppe, and Patagonian grassland/*mallín* E of San Martín de los Andes, Neuquén, a major ecotone. Hybrid *Tatochila mercedis mercedis* X *T. m. sterodice* with slight *T. m. vanvolxemii* influence eastward common in the valley; *Hypsochila ?wagenknechti* occurs above tree line and *H. ?galactodice* in the valley at nearby Junín de los Andes. *Eroessa chiliensis* and *Mathania leucothea* fly further west in the Valdivian forest. xi.1988. C, Shrub-steppe with a few small *Nothofagus* near San Carlos de Bariloche, Río Negro, in the deforested steppe-forest ecotonal zone. Now dominated by *neneo* (*Mulinum*, Umbelliferae). *Tropaeolum polyphyllum* abundant. This is the habitat of *Tatochila autodice autodice* X *T. a. blanchardii* intergrades and of *Hypsochila galactodice*. xi.1988. D, Patagonian shrub-steppe at Fitz Roy, Santa Cruz, the only definite mainland locality for *Hypsochila argyrodice*. xi.1988. E, Windswept bunchgrass steppe in the Department of Río Grande, Tierra del Fuego; habitat of *Hypsochila microdice* and *Tatochila theodice* near *staudingeri*. xi.1988. F, alpine shrub-steppe and *Nothofagus krummholz* in the Cordón Martial, Tierra del Fuego. *Hypsochila microdice* and a dwarf race of *Yramea cytheris* (Nymphalidae) occur here. xii.1988. All photos by AMS.

Plate IV. Zoogeographically important Argentine Pieridae and some of their habitats. A, upper and B, lower surfaces: 1. *Colias mendozina*, Aconcagua Provincial Park, Quebrada de los Horcones, Mendoza (across top: left, male, 30.XI.1989; center, yellow female and right, whitish female, 15.XII.1989). 2. Male *Hypsochila* from vicinity of Las Lenas, Mendoza, 3.XII.1989, showing apparent intergradation from *wagenknechti* to *galactodice* phenotypes. The two upper specimens are from >3000 m on Cerro de los Fosiles; the lower one is from a wet *vega* at 2100 m. 3. *Phulia nymphula* from the southernmost locality known in the main Andean cordillera, male (above) and female; Cerro de los Fosiles, near Las Leñas, Mendoza, 3100 m, 3.XII.1989. 4. *Colias vauthierii* from the northernmost known locality, Arroyo El Deshecho, near Las Lenas, Mendoza, 2100 m, 5.XII.1989, male (above) and female. 5. Male *Tatochila inversa*, Abra Infiernillo, Tucuman, 26.XI.1989, the only ♂ specimen of the first brood known to me. C, D, Habitats of *Colias mendozina* in Quebrada de los Horcones, Aconcagua Provincial Park, Mendoza. *Phulia nymphula* and *Hypsochila wagenknechti wagenknechti* also fly here; 3300–3900 m. XII.1989. E, Habitat of *Hypsochila* near *galactodice*, near Las Lenas, Mendoza, 3000 m, XII.1989. F, Alpine steppe near summit of Cerro de los Fosiles, near Las Leñas, Mendoza, 3400 m, habitat of *Hypsochila* near *wagenknechti* and of *Phulia nymphula*. XII.1989. (Figs. A and B by S. W. Woo; remainder by AMS.)

1♂ Tolar Grande, Salta, 3525 m, 15.I.1978 (M. Vargas) (ML)
(ii) The Quichua District
(a) Salta highlands
3♂ Cerro Zapallar, Salta, 28.XI.1989 (AMS)
(b) The *Sierras Pampeanas*
2♀ El Manchal, Catamarca, 4000 m, I.1959 (ML)
1♀ Cerro Muñoz, Tucumán, 4000 m, I.1959 (ML)
1♂ Summit above Abra Infiernillo, 3450 m, 26.XI.1989 (AMS)
6♂ 5♀ Huaca Huasi, Tucumán, 4150–4250 m, 2.III.1977, 4.IV.1977, 14.VII.1977, 1.IX.1978, 23.IX.1978, 28.IX.1978 (all S. Halloy and E. Domínguez) (ML)
(iii) The Cuyo District
25♂ 5♀ + 1 mosaic gynandromorph (Fig. 21), Las Cuevas to Puente del Inca, Mendoza, 31.X–1.XI.1988 (AMS)
16♂ 20♀ Arroyo de Agua Negra, San Juan, above 3200 m, 3.XI.1988 (AMS)
+ 28 additional specimens from the Paso Bermejo, Mendoza (MR, ML, BM, AMS)
4♂ 1♀ Cerro de los Fosiles, 3100 m, near Las Leñas, Mendoza, 3.XII.1989 (AMS)
3♂ Cerro de los Fosiles, 3300–3400 m, Mendoza, 3.XII.1989 (AMS)
(iv) The Cordón del Viento
1♂ Cordón del Viento, Neuquén, 3700 m, 28.I.1985 (AMS)

The Problem of *Phulia aconquijae* Jörgensen

Since its original description (1916), *Phulia aconquijae* has generally been synonymized to *nymphula* — beginning with Breyer (1939), who used it in a subspecific sense. Field and Herrera (1977) state that "a study of the original description and of topotypes show that this name is a junior synonym of *Phulia nymphula nymphula*." In taxonomy as in jurisprudence, however, the reasoning leading to a conclusion of fact must be spelled out before the conclusion can be accepted, and in this case it was not. Field and Herrera were unable to locate any definite material from the type-series, but state that "Topotypes are present in the collection of the National Museum of Natural History...and indeed...may represent syntypes (although they are not so labeled). A lectotype designation is not needed at the present time." The reader cannot reconstruct how Field and Herrera dealt with the differences identified by Jörgensen between his "new" species and *P. nymphula*.

Jörgensen was an unusually meticulous observer, and the question of how he came to erect a synonym of the well-known, widely-distributed *P. nymphula* has never been addressed. The clue lies in the description. Jörgensen knew, or thought he knew, *P. nymphula* from Bolivia, and used it as a comparison in his diagnosis of *aconquijae*. Although he gives a very precise description of the wing phenotype, it is clear that for him *the* critical character was the venation. He says (1916, p. 517):

"This new species much resembles *P. nymphula* Stgr. from Bolivia, but distinguishes itself beyond differences of color and pattern principally in that the second radial vein (as in the genus *Andina* Stgr. = *Piercolias* Stgr., AMS) issues directly from the subcostal and not, as in the other species, united for a while with it (in one example of the female they are united a short distance)."

This makes no sense if one has learned only the Comstock-Needham system of naming the wing veins. But Jörgensen is using an antique terminology which employs some of the same names as Comstock-Needham *but for different veins*. The "second radial vein" as used here means our M_2, which is entirely free in *Piercolias* and in *P. nymphula* but anastomosed with R_{3+4+5} in *Phulia paranympha* Stgr. from Bolivia. The "subcostal" is not our Sc, but the combined radials. Thus we may infer that Jörgensen had Bolivian *paranympha* misidentified as *nymphula*, and concluded that his material — true *nymphula*, in fact — was different and new. The source of this confusion was traced by Breyer (1939) and echoed by Field and Herrera (1977) but only in reference to the name *Phulia reedi* Giacomelli (1918). Giacomelli's type series was from Las Cuevas in the Paso Bermejo, Mendoza, that most accessible of high-cordilleran sites. Staudinger (1894) had misidentified Chilean material as his own *paranympha*, when it was actually *nymphula*. Giacomelli reasoned that his material from Mendoza was not *paranympha*, hence had to be something new! In 1924 Röber proposed the replacement name *joergenseni* for the Bolivian insect, if in fact Jörgensen's insect *aconquijae* were synonymous with *nymphula* (type locality Coquimbo, Chile): after all, wouldn't that leave the Bolivian species nameless?

In fact, *aconquijae*, that is, *Phulia* from the *Sierras Pampeanas*, like some of the sympatric *Tatochila* is perhaps marginally taxonomically recognizable on the basis of the very small size of September–October material, electrophoretic and early-stage characters. The populations in areas i–iii all differ at this (subspecific) level, but adult wing phenotyes are extraordinarily variable in all of them. (The Cordón del Viento population is known only from my specimen and an independent collection by MG, which I have not seen.) If it is ultimately desirable to name these, *nymphula* is the correct name for the Cuyo District populations, *aconquijae* remains available for the Calchaquíes-Aconquija animal, *reedi* is unambiguously a synonym of *nymphula sensu stricto*, and there is no name available (unambiguously) for the *puna* populations.

Field and Herrera present the type-locality information for *aconquijae* in a confusing way. On p. 19 they quote Jörgensen's list of localities (from his p. 517; Cerro Medio through Cerro Negro) without mentioning La Ollada, which Jörgensen finally refers to 16 lines later. Their list of material examined (p. 20) includes among localities *only* La Ollada as possible topotypes, as referred to in the text. Breyer (1939, p. 46) refers to Jörgensen's "types": "Ein Vergleich unserer Tiere mit der Typen Joergensens..." Breyer's collection is at La Plata, where there are five Jörgensen *Phulia*, none identified as the type of *aconquijae*. They are in drawer 83 of the "Petrowsky collection" cabinet and are not listed as types in the type file. All have Jörgensen MS labels and they are from: Cerro Medio, 2♂ 1♀, 13.II.1915 and La Ollada, 1♂ 28.III.1916, 1♀ 17.III.1916. In MR are several more Jörgensen specimens bearing MS labels "*aconquijae n. sp.*" and "La Ollada/Catamarca," almost certainly syntypes. All of these are normal *Phulia nymphula* from the *Sierras Pampeanas*, not a new species.

Jörgensen himself notes variation in his venation character. The venation of several *Phulia sensu lato* appears quite labile. Very small *P. nymphula*, such as occur at Huaca Huasi in September, may have R_{3+4+5} crowded at the very apex of the FW, where it diverges from M_1, looking like it is about to be pushed off the apex altogether. This in fact has happened in *Infraphulia madeleinea* Field and Herrera from Peru, but Shapiro (1985) reported a female from the Department of Junín (above Lima) which had conserved the "lost" vein on both FW, and Lamas (*in litt.*, 15.XII.1986) reported a male from Pampa Galeras, Ayacucho with a 3-branched radial on one FW and 2-branched on the other.

The S extent of *P. nymphula* remains conjectural. The Cordón del Viento population, at 37°S (70°30′W), is considerably S of the farthest S record in the main *cordillera* (35°04′S). We have not found *P. nymphula* in seemingly suitable habitat in the Maule district, Chile (36°S, S.P. Courtney) or at Copahue, Argentina, above Chos Malal (37°45′), where *T. m. mercedis* leaks over on to the E slope.

Genus *Eroessa* Doubleday

Eroessa chiliensis Guérin

This remarkable species barely enters Argentina at the extreme W ends of the Nahuel Huapí (Río Negro) and Lanín (Neuquén) National Parks. Peña (1975) records it simply from Neuquén, but its potential habitats occupy less than 1% of the area of the Province. I have seen it between Puerto Blest and Laguna Frías in the Nahuel Huapí park. Jörgensen (1916) and Breyer (1936, 1939, 1945) were apparently unaware of its occurrence in Argentina and Hayward (1950) as usual cites only the Province, Neuquén. Schajovskoy, who was resident naturalist in the Lanín Park, knew it well and found it at Quechuquina (40°10′S, 71°35′W). MR contains a seemingly reared Schajovskoy male from there, dated 5.XI.1952. MLP has a male from San Martín de los Andes, Nqn., 27.I.1941 (R. P. Bilardi). The life history has been published (Angulo and Weigert 1974); Wagenknecht (1968) offered notes on the behavior and ecology of the adult. The host plant has been reported in print only by Peña (1975), who identifies it as *Flotovia* (= *Dasyphyllum*) *diacanthoides* Cabr., a Composite of the primitive endemic tribe Mutiseae. It is a shrub or small tree, known locally as *Palo Santo*, and is typical of the Valdivian Tertiary relict rain forest (Ringuelet 1955) — one of the oddest hosts recorded for any Pierid in the world and thus seemingly underscoring the antiquity and taxonomic isolation of *Eroessa*.

Genus *Mathania* Oberthür

Mathania leucothea Molina

Another essentially Chilean species, in this case not restricted to the Valdivian forest but extending far north in *matorral* in the *precordillera*. In Argentina it occurs in the same areas as *Eroessa* but penetrates somewhat farther eastward — its range may have contracted as a result of 19th-century deforestation in the Lake District. Schajovskoy collected it frequently at Pucará in the Lanín National Park (5.XI.1958, 30.XI.1960, XII.1950, etc., MR) and I have seen it at Cerro Catedral near Bariloche as well as further W, and once in the hills just SW of the city limits. The hosts are mistletoes ("Quintral," *Phrygilanthus* = *Tristerix tetrandus* Ruíz and Pavón, Loranthaceae), which are common near Pucará. For aspects of its biology, see Courtney (1986).

Genus *Colias* Fabricius

Colias ponteni Wallengren = *C. imperialis* Butler

This biologically very important species remains "lost" since the original series was collected, and is discussed here because of the possibility it may yet turn up in Fuegia. G. Lamas writes (*in litt.*, 13.V.1981): "*Ponteni*'s type locality is 'Honolulu,' (collected by the Eugenies Expedition; a gross mistake), and the type locality of *imperialis* is 'Port Famine' (collected by P. King?). Port Famine is Puerto del Hambre, Magallanes, Chile (53°38′S, 70°56′W), which is S of Punta Arenas; the frigate 'Eugenies' was in Port Famine from 31.I to 2.II.1852, and *ponteni* was probably collected on an excursion the scientists aboard made to Mt. Tarn." Cerro Tarn (819 m) is right by the coast just S of Puerto Hambre. Apparently no one has seen *Colias ponteni* alive in over 137 years! Nor has anyone visited the presumptive type locality to look for it, though I have assiduously searched meadows with clover and vetch in various parts of Argentine Tierra del Fuego. Any Lepidopterist visiting the region should look for it. It is undoubtedly the morphologically most primitive *Colias* known, a living — or recently extinct — fossil (Petersen 1963, Berger 1986).

H. Descimon has raised (*in litt.*) the intriguing possibility that the Hawaii-Fuegia confusion arose over the South Sandwich Islands, one of the Falkland Islands Dependencies in the South Atlantic, — "Sandwich Islands" being an antique English name for Hawaii. These islands are so remote and isolated (latitude 56° to 59°S, longitude

26°15′W) and have such a harsh climate that the occurrence of any butterfly there would be extremely remarkable.

Colias vauthierii Guérin

This widespread and common Patagonian and Chilean species extends N into the transition zone between Patagonia and the Cuyo. Hovanitz (1970) claimed a new N record in agriculturalized *mallines* at Plottier in the valley of the Río Limay, Neuquén, 8.XII.1970. (There are no Plottier specimens in the Hovanitz collection at CAS: the only Argentine material is a series from "Coyaique," 14.I.1967, which could be either Coy Aike, Santa Cruz, or Coihaique in the pass between Santa Cruz and Aisén (Chile).) Breyer (1939) quotes Köhler for "Río Agrio" (p. 50). In Neuquén I have three N collections of this species: Aluminé (16.I.1981), Loncopué (8.XI.1988), and Chos Malal (28.I.1985). Loncopué is in the Río Agrio drainage.

Hayward (1973, p. 123) records this species from "Mendoza." Although no substantiating specimen has turned up, on 3.XII.1989 I found *C. vauthierii* common on *vegas* in the Valle de Las Leñas in southern Mendoza at 2100 m. This is a remarkable range extension which graphically illustrates the interdigitation of the high-Andean and Patagonian biota in the Cuyo. Two specimens from this population are shown on Pl. IV; they are completely "typical."

C. vauthierii and *C. lesbia* Fabr. co-occur at Chos Malal with no trace of interbreeding and apparently have a fluctuating zone of overlap across central Patagonia. Strays of *C. lesbia* occur regularly S to San Martín de los Andes, Neuquén and San Carlos de Bariloche, Río Negro and somewhat less often to Esquel, Chubut. *C. lesbia* is abundant in eastern Chubut (Trelew, Rawson, Puerto Madryn), breeding and perhaps overwintering at Comodoro Rivadavia since it has been taken there in spring.

Colias flaveola Blanchard (Fig. 22; range 10D, 11D)

Nominate *flaveola* has been considered a Chilean endemic, and no supposed subspecies are reported from Argentina. On 3.XI.1988 I collected 18♂ 4♀ *flaveola* above 3350 m in the Arroyo de Agua Negra, San Juan (30°12′S, 69°51′W) in typical habitat — high-altitude *vega* (sedgy stream bottom) (Pl. II–D). This locality is directly across the crest from the classic localities in the Province of Coquimbo, Chile. The Argentine material does not differ phenotypically from series from Baños del Toro, Coquimbo, 3800 m, 7.I.1972 (Hovanitz) and Río Seco, 11.III.1936 and 20.II.1937 (E. P. Reed) (all CAS). The Chilean skipper *Hylephila isonira mima* Evans (Hesperiidae) was taken in the Arroyo de Agua Negra the same day.

Colias mendozina Breyer (Plate IV; range Figs. 10D, 11D, 24)

Breyer (1939, p. 52) described this entity as *C. blameyi* f. *mendozina*. The text of his description follows: "Ist eine Abart, die sich durch starke Verbreitung der schmutzigen Gelbfärbung auszeichnet. Vorderflügel mit breitem schwarzen Apex und Aussenrand, von dem aus die breit geschwärzten Adern nach innen ziehen und mit dem Diskalfleck verfliessen. Wurzel hinten und Innenteil des Innenrandes intensiv schwarz. Hinterflügel am vorderen Tornus breit geschwärzt; Diskalpunkt rein gelb. Wurzel und Zellbasis tief schwartz. Unterseite zeichnungslos; Hinterflügel-Diskalfleck gelb und Wurzelfeld verdunkelt. — Typus und Paratypus in unserer Sammlung. — Habitat: Mendoza auf 3000 m Hohe, leg. Breyer." ("A variety, distinguished by the strong diffusion of the dirty yellow color. Forewing with broad black apex and outer border, from which the broad blackish veins reach inward and blend with the discal spot. Base and inner border intense black. Hindwing with front angle broadly blackened; discal spot pure yellow. Base of wing and cell deep black. Underside without pattern; hindwing discal spot yellow and basal portion darkened. — Type and paratype in our collection. — Habitat: Mendoza at 3000 m, leg. Breyer.")

The existence of this entity has been studiously ignored, e.g. by Berger (1986). On biogeographic grounds the occurrence of a "variety" or subspecies of *C. blameyi* Jörg. in the highlands of Mendoza seems unlikely, since the entire group to which that taxon belongs is tropical or subtropical except *C. flaveola*, which occurs S of the range of *blameyi* itself in Argentina and thus would apparently intervene between it and any putative subspecies in Mendoza. The description is barely adequate to allow one to visualize the animal. At the end of November 1989 I examined the three specimens of *mendozina* in the Breyer collection at MLP. The two types are faded and show evidence of having been mildewed. Both are labeled "Argentina Prov. Mendoza" and one bears a pink "TYPUS," the other a green "PARATIPUS" label. The third specimen is much brighter and fresher-looking, but has been broken and glued with a heavy, opaque material. It is labeled (in English) "Las Cuevas F.C.T. 15.I.1904/W.M.B. Seen also at Puente del Inca." F.C.T. presumably means "Ferrocarril Transandino." These specimens are clearly distinct from any other Andean *Colias* and not particularly close to *C. blameyi*. Only a few days after examining them I found *C. mendozina* flying in the Mendoza highlands! At present I have 9 specimens, all from Quebrada de Los Horcones (Lower Horcones to Confluencia), Parque Provincial Aconcagua: 1♂ 30.XI.1989 and 4♂ 4♀ 15.XII.1989, all AMS. A male and both color forms of the female are shown on Plate IV.

C. mendozina is easily told from other Andean *Colias* by its odd, almost mustard-yellow ground color (even the pale females are of a different hue than other Andean ones), small size, and short, almost truncate, forewing. The dorsal black suffusion is weak and less extensive than in other taxa, scarcely more than in *C. flaveola*. The discal spot is large and rounded on males and variable on females. The large blackish area at the apex of the hindwing above and the brownish basal suffusion below are also distinctive. Oviposition was observed on a small, tufted, blue-flowered *Astragalus* (*arnottianus* (Gill.) Reiche) (det. R. Barneby).

The known localities for *C. mendozina* are on the so-called "normal route" used by climbers to access Cerro Aconcagua. Fig. 24 reproduces a map of the Parque Provincial with known habitats of appropriate type indicated, that is, *vegas*. I suspect *C. mendozina* will eventually be found on all such *vegas* up to at least 4000 m. Conversations with climbers and guides indicate many of them are familiar with the animal.

Whether *C. mendozina* will eventually be found outside the Aconcagua Park is highly doubtful. Although the vegetation along Highway 7 is commonly taken as typical of the montane *Cuyo* (e.g. Wingenroth and Suárez 1983), there is actually a rapid turnover in both floristics and community composition between the *C. flaveola* locality in San Juan and the vicinity of Las Leñas in southern Mendoza. *C. mendozina* could thus easily be a narrow endemic (like *C. flaveola*). Since it formerly and perhaps still could be found at Las Cuevas it should be looked for on *vegas* across the border in high-altitude Chile.

A formal redescription will be published at a later date.

The evolutionary and biogeographic history of this animal should be of great interest. If it is truly related to *C. blameyi*, it must represent an Interglacial stranding of an essentially tropical stock which managed to adapt to the strong temperate seasonality (including persistent snow for 5–7 months) of the Paso Bermejo. Its existence under our noses in the most accessible high-altitude locality in the Argentine Andes is a potent reminder of our extreme ignorance.

Colias blameyi Jörgensen — *C. weberbaueri* Strand (Fig. 10D, 11D)

MLP contains an original Jörgensen specimen — a female dated 13.II.1915 from Cerro Medio, as well as later topotypes (very dark ♂ and ♀, Cerro de la Mina, Depto. Tafí, Tucumán, IV.1933, no collector).

The life-history of this species has been described by Shapiro (1989b). Its distribution resembles the N part of that of *Phulia nymphula* or the high-altitude *Tatochilas* — *puna*, Quichua District and *Sierras Pampeanas*. Some representative data: Quebrada Carapunco, Abra Infiernillo, Pcia. Tucumán, 12♂ 3♀ 26.XI.1989, 35♂ 10♀ 20.I.86 (all AMS); Abra Molina, Cerro Zapallar, Salta, 18♂ 7♀ 28.XI.1989, 5♂ 7♀ 22.I.1986 (all AMS); 1♂ 2♀ Valle Encantado, Salta, 22.I.1986 (AMS); 13♂ 3♀ Esquinas Blancas, Jujuy, 7.II.1984 (AMS); 1♂ Abra Pampa, Jujuy, 7.II.1984 (AMS). The Abra Infiernillo and Abra Molina data unambiguously indicate at least two, perhaps three broods, the first beginning immediately upon the onset of the rains (in November the *Astragalus* are just beginning to grow and bud).

Variation among populations is quite noticeable. All the Argentine material I have seen has at least traces of an androconial patch in the male, but material from the *puna* is colored more like Bolivian *C. weberbaueri* than is topotypical *blameyi* from the *Sierras Pampeanas*. CAS has long series of *weberbaueri*. In a group of 9♂ from "50 km S Oruro, 3700 m, 14.I.1972, W. Hovanitz," 7 have no androconial patch, 1 has traces, and 1 has a well-developed patch and is indistinguishable from Jujuy males. This site is roughly 475 km NNW of Abra Pampa. Further study will almost certainly demonstrate the conspecificity of these taxa. It is quite unusual to find such variation in a secondary sexual character and potentially of great evolutionary interest. Presence of androconia appears primitive relative to absence in *Colias*. This, however, does not necessarily imply S-to-N movement in the history of the green complex.

Genus *Eurema* Hübner

Eurema deva Doubleday

A common, weedy, highly dispersive species in N Argentina, reaching far S as strays in much the same manner as *E. lisa* Bdv. & LeC. in North America migrates N-ward in summer. My S-most records are Bariloche, Río Negro, 17.I.1984 and Caleta Olivia, Santa Cruz, 9.XII.1989. It also reaches high elevations, such as Abra Infiernillo, Tucumán, 3300 m, 20.I.1986. All of these were females.

Genus *Teriocolias* Röber

Teriocolias riojana Giacomelli

This altitudinal disperser apparently reaches the summits in the *Sierras Pampeanas* remarkably early in the rainy season, as single females were taken at Abra Infiernillo, 26.XI.1989 (Tucumán) and Cerro Zapallar, 28.XI.1989 (Salta) (both AMS). No known host plants were available in either site so early in the year.

Discussion

The raw data for an analysis of the zoogeography of the faunas and taxa reviewed here are based on collection records. Tables 1–2 present the species compositions of 25 selected faunas in Argentina and Chile. They are variably well-studied; richness is not pro-rated by area. Thus the term "Puna de Atacama" covers a vast and heterogeneous area — partly *puna* and partly cordilleran — which overall has been visited by perhaps ten collectors and is too poorly known to be subdivided yet, although it contains great riches and much endemism. Chos Malal, Aluminé and Loncopué are dots on the map which have been visited by only one or two collectors, but frequently and are thus well-known. Much of the Argentine data used here is explicitly presented in the previous section. That which is not is based on precise and reliable sources, including the collections enumerated in the Acknowledgments, the author's collections at U.C. Davis (=AMS), and a handful of publications. By and large, the Argentine literature is much too vague and full of misidentifications to be credible for use in analytical biogeography. The Chilean data are from Herrera and Field 1959, Field and Herrera 1977, Herrera 1953 and 1970, and unpublished data provided by Herrera, S. P. Courtney, and AMS. Chilean biogeographic concepts are from Artigas (1975), Peña (1966), Davis (1986), Irwin and Schlinger (1986), and Hueck and Seibert (1972). Unsatisfactory as the data may be in scope and repeatability, they are far better than for any other part of the Andean region except for the Satyrid faunas studied by Michael Adams in Colombia and W. Heimlich in the Southern Cone.

Many indices of faunal similarity exist, which allow one to compare areas and to construct a hierarchical "classification," or dendrogram, of faunas based on shared elements (species, subspecies). Two recent reviews (Janson and Vegelius 1981, Hubálek 1982) have identified Sørensen's (1948) coefficient as one of the best if not the best in terms of objectivity and properties. (Although Sánchez and López-Ortega, 1988, disagree, their objections do not apply to these faunas.) From the values in Table 3 a dendrogram can be derived by cluster analysis (Fig. 23). This approach allows an easy visualization of overall faunal affinities, but its use for historical reconstruction is limited, as in all phenetic methods.

The dendrogram shows few surprises, but does offer some useful insights. It emphasizes the distinctness of the central-Andean high-altitude faunas of the N from the Patagonian faunas, at least at the taxonomic level used here. (The extremity would have been softened had subspecies not been weighted equally with full taxonomic species in the analysis.) The only northern fauna falling outside this cluster is the Valles Calchaquíes, the arid depression lying W of and in the rain shadow of the *Sierras Pampeanas*, which represents the N-most extremity of the *monte* both floristically and faunistically (Hayward 1955b) — its fauna is small and depauperate and quite similar to that of the Uspallata Valley (Precordillera Mendocina) in the Cuyo District; none of the highland entities, even the altitudinal migrants, descend into it. (If *Ascia monuste* had been counted, it would count as a regular migrant crossing both highlands and valleys, cf. Hayward 1931.) These two localities in turn cluster with the Gulf of San Jorge (Comodoro Rivadavia), which has the rarefied desertic fauna at the opposite end of the *monte*. The analysis does not include the *prepuna*, but its fauna is virtually identical to that of the Valles Calchaquíes. This fauna thus wraps around the seasonally arid lower reaches of all the highlands in western Salta and Jujuy and in Catamarca and La Rioja.

Farther S, the N-Patagonian localities (Cordón del Viento, Loncopué, Aluminé, Bariloche, San Martín) cluster stair-step fashion. The sequence is reversed in the S because of the heavier Chilean influence at San Martín. This emphasizes that faunal turnover is not a simple function of distance from sources. In the Patagonian Andes the passes provide variably effective access for both low-altitude moisture and the Valdivian biota. From Bariloche south the Chilean contribution is less, not because the passes are more difficult but because the butterfly fauna becomes sparse in the very wet W-slope climates.

One of the more interesting clusters is of Chos Malal with the Chilean Central Valley; the latter has a conspicuously Patagonian element in the form of *Colias vauthierii* (and *Yramea cytheris*, etc.) not easily predictable from climatic data. This is explicable under the dispersal model of Caviedes and Iriarte (1989), discussed later.

In order to attempt reconstructions of specific histories, one need take into account the identities of individual taxa shared and not shared among faunas, the geographic distributions of individual taxa and the relationships of the ranges among related taxa, the degree of taxonomic differentiation and endemism in different regions, and the repeating patterns of distribution of different lineages, corresponding roughly to the "generalized tracks" of Croizat (1964; see also Craw 1982). Ultimately the phylogeny of the individual genera and of the Andean Pierini will be resolved, but so ambitious an undertaking must await much more data on "biology." Within the area covered by this study, however, patterns are already evident and in some cases their causation may be inferred. This returns us to the objectives enumerated in the Introduction.

The Uniqueness of the Puna. The high-altitude *puna* of NE Chile has a remarkably large and diverse fauna of Pierini, much of it endemic at the species level, which appears to dilute rapidly once one crosses the crest into Argentina. Far NW Argentina is very poorly collected due to its inaccessibility, difficult topography and harsh climate. Large areas are not only roadless but essentially uninhabited. To my knowledge no one has ever collected in the Sierra de Calalaste or farther W in N Catamarca, or even from Highways 27 or 17 in W Salta or from Highway 70/b in Jujuy. This is very bleak, barren terrain with many salt flats. The interesting Pierini are to be expected on bogs and rocky summits, not on the *tola*-covered flats through which most of the roads go. Thus, off-road vehicles or pack animals are required. When we do this work, I imagine we will extend the ranges of at least part of the Chilean *puna* fauna, perhaps including *Infraphulia ilyodes* Ureta, *Pierphulia rosea* Ureta, *Hypsochila penai, Tatochila mariae* Herrera, and *T. distincta fieldi* Herrera — just as the range of the genus *Hypsochila* will surely be extended into Bolivia, where there are no records today.

The very rich Chilean *puna* fauna is a S-ward extension of that of the Peruvian *altiplano* and seasonally dry high *Sierra*. The greatest faunal diversity of Andean Pierini is between the Peruvian Departments of Junín and Cusco, with perhaps the maximum diversity of *altiplano* taxa in Arequipa and of *Tatochila* in the complex ecogeography incorporating *yungas*, *jalca*="*páramo*" in the Peruvian sense (which is not the same as its use in Colombia, Venezuela and perhaps Ecuador), and *altiplano* within short (air) distances. These faunas appear to rarefy to the E in Bolivia, but collecting has been so spotty that little can really be said. Within the *puna* and *altiplano* the small Pierini (except perhaps *Phulia nymphula*) are restricted to bogs or bog margins at least in dry season (Shapiro 1985, 1986a, Shapiro and Courtney 1986). This limits their dispersal and seems to have promoted local differentiation and subspeciation. *Infraphulia madeleinea* females are very poor fliers — *I. ilyodes* are somewhat better — and electrophoretic as well as morphological data suggest that different allopatric populations of small pierines are evolving in isolation from one another. Despite seasonal variability, many of the bogs are certainly of Pleistocene age and, like Nearctic bogs supporting relict butterflies, have been able to sustain isolated populations for millenia. The bog illustrated by Weberbauer (1945, pl. XIII, p. 391) at Morococha (4500 m) has an exceptionally rich fauna and had not changed visibly in the 80-odd years since the picture was taken; pasturage does not appear harmful.

Phulia nymphula is the most ecologically versatile and dispersive of the small Pierini, in Peru (Pérez 1982, Lamas and Pérez 1983) as elsewhere; it is not surprising that it is so widely distributed in N Argentina (see below).

The Quichua District and the Sierras Pampeanas. There is great similarity between the high-altitude faunas of Salta and Jujuy and that of the Pampean Sierras (*Cumbres Calchaquíes — Sierra de Aconquija*) in Tucumán and Catamarca. The affinities of these high-altitude faunas, in turn, are with the *puna*. *Phulia nymphula* (*aconquijae*) is very instructive. In the *puna* above the Quebrada de Humahuaca, *P. nymphula* flies at the same elevation (albeit often in different habitats) as *Tatochila m. macrodice, T. d. distincta, T. inversa*, and *C. blameyi*. In the *Sierras Pampeanas* it occurs mostly above those species — mostly above 4000 m, though descending in autumn (March–April) as low as 3100 m (as noted by Jörgensen, 1916). It is not clear whether this altitudinal stratification in the *Sierras Pampeanas* reflects climatic differences or merely the occurrence of *Phulia* habitat — sandy alpine grassland-steppe with only very low plants — mainly above the *Tatochila* concentrations, which occur on rocky substrates below the glacial-pothole landscapes. As noted under that species, Pampean Sierra *P. nymphula* might be recognized as a subspecies. The same is true of *T. inversa*, *T. distincta* and perhaps even *T. m. macrodice*, and, as noted above and in Shapiro (1989b), topotypical *Colias blameyi* seem to grade into *C. weberbaueri* both NW and N of the *Sierras Pampeanas* in the Quichua District. The distances are not great (100–150 km) between the highlands of Salta and Jujuy and the *Sierras Pampeanas*, but the ecological barriers are formidable. These barriers are traversed annually by *Ascia monuste automate* and perhaps by *Teriocolias*, as well as by many other seasonally migrant Lepidoptera. It seems unlikely that any of the true high-altitude Pierids are presently moving between the ranges. This might have been much easier in the Pleistocene. Halloy (1978, 82, 83) provides the most in-depth description and analysis of the Cumbres Calchaquíes from ecobiogeographic, physiological, and paleoclimatic perspectives. He finds that from a late Pleistocene glacial maximum, they are continuing to rewarm, and the snow line is still regressing upslope. If we know little of the regional biota before the Quaternary, we can still infer that the differences between populations in the *Sierras Pampeanas* and the main *cordillera* and *puna* are unlikely to antedate the later Quaternary. Using this inference, it may be possible to calibrate "molecular clocks" for the Andean Pierids more precisely than has been done heretofore. All these mountains attained alpine heights only in the Plio-Pleistocene. Are the insects conceivably any older?

It is very striking that the genus *Hypsochila* appears to be absent in the well-collected *Sierras Pampeanas*, eluding Giacomelli, Jörgensen, Hayward, Halloy, Domínguez, and me. *Hypsochila* is also unrecorded from Cerro Zapallar (Cuesta del Obispo). In fact, there are no records to connect up *H. w. wagenknechti* of the temperate cordillera of the Cuyo District with *H. w. sulfurodice* of the *puna* (San Antonio de los Cobres, Quebrada de Humahuaca). This is probably significant. It also casts doubt on the true conspecificity of the *galactodice*-like specimens from the *puna* and those from the main range of that entity far to the S in Patagonia. Indeed, it is by no means certain that *wagenknechti* and *sulfurodice* are conspecific. The zone where no *Hypsochila* occur is the zone of heaviest seasonal precipitation in the uplands, precisely where the tropical northeasterlies are wrung out at the head of the *yungas*. This may well be a limiting factor on *Hypsochila*, which is happy in the extreme aridity of the summits above Abra Muñano. It may also contribute to the upslope displacement of *Phulia* in the Cumbres Calchaquíes.

The seasonal presence of *Tatochila orthodice* and *stigmadice* in these same high-precipitation areas reinforces the impression that contemporary climate exerts strong control over contemporary distributions. These are true *yungas* species, which do occur in the wetter parts of the true *puna* close to the tops of the big canyons, without penetrating into *tolares*.

In summary: the wet alpine reaches of the *Sierras Pampeanas* share their fauna of *Tatochila* and *Colias* with the wetter parts of the Quichua District in Salta and Jujuy; the altitudinal distribution of

Phulia is somewhat skewed; and *Hypsochila* is absent from both, though common in the drier parts of the Quichua District and in the *puna*. These patterns were probably created in the late Pleistocene and are controlled today by micro- and mesoclimate distributions.

Connections Between the Cuyo *and the Quichua District and* Puna. The fauna of the high cordillera in Mendoza and San Juan is depauperate. I have not included *Colias mendozina* in the analysis only because it was rediscovered as this paper was about to go to press. It is the most unusual faunistic element in the Paso Bermejo but at present we cannot say whether it is more closely related to *C. blameyi* of the *puna* or to *C. flaveola*. (It is striking that if *C. blameyi*, *flaveola* and *mendozina* are combined, their range approximates that of *Phulia nymphula sensu lato* which, as noted previously, is differentiated into several segregates adapted to either tropical or temperate seasonality.) The only true *puna* element found in the alpine elevations of the *cuyo* is *Phulia nymphula*. *Hypsochila wagenknechti* is present as a presumptive sister-subspecies of the *puna sulfurodice*, and there may be either *T. m. mercedis* — *T. m. macrodice* hybrids or intergrades in San Juan. *Colias flaveola* seems limited to a very narrow latitudinal band on both sides of the Andes. Although Descimon (1986) treats it as potentially conspecific with *blameyi*, *weberbaueri*, etc., there is little reason to do so. Thus, the very rich *puna* Pierid fauna rarefies very rapidly once the regime of the tropical "Bolivian Winter" is replaced by the true cordilleran winter with a more or less continuous snow pack which forces a several-month interruption in butterfly activity. Since *Phulia nymphula* has adapted its life-cycle to the mendocino winter it is unclear what limits its range farther S, but it seems to drop out before the Maule district. *H. w. wagenknechti* continues S to Laguna del Maule and seems to segue into *H. galactodice* in NW Patagonia in a manner which remains unclear (see below). The *cordillera* was very heavily glaciated in the *cuyo*, and at present it cannot be told whether *P. nymphula* reinvaded from the NW after deglaciation or had been depressed to lower elevations, such as the *precordillera* above Uspallata, and reinvaded upslope.

The Las Leñas fauna (35°04′S, 70°02′W) is very unusual and interesting in presenting an altitudinally-stratified mix of northern and southern elements, including *P. nymphula* and *H. wagenknechti* above 3000 m and *H. galactodice* and *Colias vauthierii* below. The same phenomena are reproduced in the Lycaenid genus *Itylos* (Shapiro, unpublished data). The habitats of *P. nymphula* on Cerro de los Fosiles are very local and specialized in aspect and vegetation. One might expect a *puna* species to occur at ever-lower altitudes to its S limit outside the tropics, but the known *P. nymphula* sites on Cerro de los Fosiles are all higher than its lowest sites in the Paso Bermejo further N, and it is not a *vega* species as it often is in the Paso Bermejo. Indeed, its habitats near Las Leñas are more like those where it has been taken in the Cordón del Viento.

The Cordilleran – Cordón del Viento Connection. This isolated, high, arid pre-Andean range, dominated by the 4710 m Volcán Domuyo, has the S-most known population of *Phulia nymphula* and also has a *Hypsochila*, unfortunately thus far known from only one male, which may be *galactodice* or *wagenknechti* or something inbetween. The distance to the nearest *Phulia* known in the *cordillera* is between 175 and 225 km. The presence of *Hypsochila* here is especially interesting in view of its absence from precordilleran ranges further N. Again, either these taxa were depressed to low elevations during the Pleistocene or colonized in the past 10–15,000 years. The distances involved imply the former as more likely, especially for *Phulia*. Thus, these high-altitude taxa may at one point have entered quite low parts of far NW Patagonia (the Payunia district), where we now find a mosaic of Patagonian and *monte* elements segregating by micro- and mesohabitat.

Geography of the Tatochila mercedis *complex.* It is quite clear that *T. m. macrodice* is the true central-Andean representative of this polytypic species, and most closely related to *T. m. arctodice* of the far N. In N Argentina as well as in Peru and Bolivia it has a remarkable ecological amplitude, occurring in both wet and very dry climates at high altitude. Its great vagility undoubtedly contributes to this, and it migrates elevationally with season in much of its range. Both it and *arctodice* are adapted to tropical seasonality, and its absence from the *cordillera* in the Cuyo District (despite the queried Mendoza record, not in Hayward 1950) is consistent with this: it has no place to go in winter and (in the laboratory) does not seem to be able to diapause. Diapause was, however, evolved as the complex invaded the temperate climates of the Southern Cone. The non-diapausing *macrodice* comes spatially very close to *T. m. vanvolxemii*, which diapauses in winter, along Highway 307 between Abra Infiernillo and Amaichá, but no actual contact has been found and the two are separated by a zone in which neither seems to occur.

Otherwise, *T. m. vanvolxemii* contacts and exchanges genes with *T. m. sterodice* and *T. m. sterodice – mercedis* hybrid populations along the W and SW edges of its range in Neuquén and Río Negro; its populations in the Mendoza *precordillera* (e.g., Potrerillos) and below Copahue and W of Chos Malal show signs of past or perhaps present introgression from *m. mercedis*, though the populations at both Mendoza and Chos Malal themselves appear pure; and the population in the Gulf of San Jorge warm pocket (Comodoro Rivadavia) presents a normal summer *vanvolxemii* phenotype but its cold-season brood displays strong *sterodice* influence. Intergrading populations in the San

Jorge District are clearly dependent on local populations of adventive Cruciferous weeds and cannot be very old — indeed, their ruderal character argues that the intergradation itself is likely to be secondary, and of recent origin.

True *T. m. mercedis* enters Argentina from Chile in NW Patagonia, but it does not seem to occur anywhere where it does not contact and hybridize with *T. m. sterodice.* Its range in Chile is basically limited to the Mediterranean climate belt, from Copiapó to Valdivia, and it does not occur in the "pampas" of NE — C Chile or approach *T. m. macrodice* closely anywhere except perhaps in Coquimbo and San Juan. The oldest museum specimens of *T. m. mercedis* from NW Patagonia date from 1939, with intergrades already present — so the phenomenon has a minimum age of some 50 yr, or 150 generations, but deforestation and land-use patterns suggest it could be at least twice that age if it in fact is a recent, man-influenced phenomenon.

Of all the Argentine Pierids, this complex most accurately mirrors the phytogeography. It also has the most extensive distribution of any Pierid, and probably any butterfly, on the continent — from central Colombia to Ushuaia, though avoiding forested and lowland-tropical habitats.

The Relationships of Fuegia and their Evolutionary Implications. Although Fuegia is recognized as a separate phytogeographic entity, its butterfly fauna is less distinct than heretofore supposed — though it has more Pierid taxa than the Cuyo District! The allegedly endemic *Tatochila* and *Hypsochila* are either also found on the mainland (*argyrodice*, *microdice*) or are clinal, with no sharp step at the Straits of Magellan (*theodice* ssp., *sterodice/fueguensis*). These facts argue against postglacial higher sea levels as responsible for isolation and differentiation-by-vicariance in the far S. But interesting evolutionary problems remain.

The Quaternary history of Tierra del Fuego is exceptionally well-known (Auer 1956, 1958, 1965, 1966, 1970). All of the mountains were glaciated; glacial retreat began some 16,000 BP. The entire vegetation of Fuegia can be assumed to have developed in this period, and it is not surprising that only 3% of the Fuegian flora of 545 vascular plant taxa is endemic; some 64% of the flora occurs N up the Andes on both slopes, 2% only on the drier Argentine side, 4% only in Patagonia E of the Andes and 8% N in Chile only (Moore 1983). The Fuegian Pierid fauna is overwhelmingly a steppe fauna; all the species occur on the Patagonian mainland in steppe, though two (*Tatochila theodice* and *T. sterodice*) also occur in the subhumid Patagonian Andes. *T. t. theodice* is recorded in Chile S to Victoria, at about the same latitude as Aluminé, but the species apparently continues S along the E slope of the Andes, grading into ssp. *gymnodice* and thence into ssp. *staudingeri* in Fuegia. The type locality of *gymnodice* is Punta Arenas, Magallanes, which further confuses the situation! *T. m. sterodice* is not recorded unambiguously in Chile at all, though again the Magallanes populations are part of a cline between it and *fueguensis*. None of this should be surprising, were the 10,000-yr-old Straits of Magellan not taken unduly seriously as a barrier. Moore (*op. cit.*, p. 33) says: "The four principal climatic and vegetation zones described in passing from N and E to S and W Fuegia. . .parallel rather closely the sequence seen N of the Estrecho de Magallanes in traversing cool temperate Argentina and Chile from the Atlantic to the Pacific Oceans. Since all plant species can only occupy areas with climatic and ecological conditions within their range of tolerance it is not surprising that some species restricted to the drier steppe areas of NE Tierra del Fuego extend N-wards in the drier parts E of the Andes. . ." The only question is whether the Pierids crossed into Tierra del Fuego before or after there was a water barrier. In any case, the taxa are both weak and young and the climate unstable (Markgraf 1985).

More interesting is the hostplant specialization of those taxa. All three subspecies of *Tatochila theodice* feed on Legumes. So does *Hypsochila microdice* (and probably also *H. argyrodice* and *H. huemul*, which seem very closely related). How are we to interpret this oddity in a Crucifer-feeding lineage? Of all *Tatochila*, *distincta* is closest to *Hypsochila* in genitalia (Field 1938, Herrera and Field 1959, Field and Ferrera 1970). This has not been resolved electrophoretically (Shapiro and Geiger, unpublished). If they were sister-taxa, one could then treat Legume-feeding as a symplesiomorphy, and Crucifer-*Tropaeolum* feeding would then have arisen independently in both lineages, and represent convergence. But this is very improbable. The fact that most pierines globally feed on mustard-oil-containing plants argues against it. So does the remarkably close resemblance of the early stages of the Crucifer-*Tropaeolum* feeding branch of *Hypsochila*, which includes *galactodice* and *wagenknenchti*, to the Crucifer-feeding *Tatochila* of the *autodice* and *mercedis* complexes. (*T. theodice* is highly divergent in its early stages, and its affinities may actually lie with the *orthodice-stigmadice* end of the genus, a notion supported by certain pattern characters and wing pigments of the adults, and karyotypes (deLesse, 1967; Shapiro, unpublished).) If Crucifer-feeding is the symplesiomorphy, Legume-feeding has originated separately as a derivative condition in both genera. It is not clear whether it arose in sympatry, however, Legume-feeding may have arisen more than once — perhaps three times — in *Tatochila*. These conundrums can be resolved only when the entire group of genera can be subjected to a thorough cladistic analysis incorporating early-stage data.

Some Legume-feeders have austral distributions. If they were derived from more northerly Crucifer-feeders this makes sense: although Crucifers extend at least as far S in Fuegia as Legumes and are actually more numerous, their distribution is very patchy and their biomass is much less than that of small vetches on the steppe. (Introduced weedy Crucifers are now extremely abundant around towns, but this is a recent condition.) Herrera and Covarrubias (1983) claim that the Andean-Patagonian Pierini are of Gondwanaland origin, however — suggesting that Legume-feeding (discovered since 1983) would represent the primitive condition. Is there any independent support for the Gondwanaland claim? The only suggestive datum is the bizarre provenance of *Colias ponteni.*

Biogeographers have failed to reach consensus over the interpretation of "centers of origin," a fact which has exposed the entire field to ridicule (Cain 1944, Croizat *et al.* 1974). The location of an endemic primitive taxon is not a reliable indicator of a center of origin, because primitive forms often survive in isolated regions far from where they originated (supposedly because of a lack of competitors). Any biogeography text gives several examples, the Tuatara (*Sphenodon*) being one of the commonest citations.[4] *Colias ponteni* is, genitalically, easily the most primitive living (or recently extinct?) member of its large genus. (It was classified by Peterson, 1963 in its own genus, *Protocolias.*) Is its inferred endemism in Tierra del Fuego an indicator that the entire genus is of Gondwanaland origin? Its nearest relative seems to be *vauthierii*, which occurs in Patagonia and the Central Valley of Chile. Electrophoretically all the South American *Colias* seem to cluster together, including *vauthierii* (Descimon and Geiger, pers. comm.). There is no indication in these data that *vauthierii* is the stem-species of the monophyletic Andean group inferred by Descimon (1986), or the group's sister-taxon. Nor do the global data on *Colias* support a Gondwanaland origin for the genus: the only other austral *Colias*, *C. electo* L., has a spotty relict distribution in east, central and southern Africa and belongs to a Palearctic species-group.

The Limits of Patagonia. The traditional political limit of Patagonia is the Río Negro, but there has never been a formal jurisdiction named "Patagonia" and in any case the biota on one bank of the Río Negro does not differ from that on the other. The Argentine phytogeographical literature attempts to define boundaries in the low, undulating relief of N Patagonia where it contacts and intergrades to the *monte* and *pampa* (Morello 1958, Ragonese and Piccinini 1969). From a pierid standpoint, Patagonia extends into the river bottoms of NW Neuquén (the Payunia district) which form the N limits of *Colias vauthierii* and some

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[4] This concept was articulated at least as early as 1752 by Maupertuis, who wrote with reference to the alleged occurrence of "giants" in Patagonia (Tehuelches or Ona) and "dwarves" in the north-polar regions (Eskimos): "If there is truth in what the travelers tell us of the Strait of Magellan and the lands of the far North, the races of giants and dwarves settled there because of the fitness of the climate or, what is more likely, because. . .they were driven to those regions by other men, who feared the giants or scorned the pygmies. . ." (*Origine des Animaux*, p. 266) Although the Patagonian giants were ultimately debunked (Adams 1962), the existence of *Colias ponteni* in the fairly recent past is supported by a handful of specimens.

Lycaenids and Hesperiids as well, and form part of the *Tatochila mercedis-sterodice-vanvolxemii* intergradation zone. In the reciprocal sense, the *monte* and *pampa* penetrate Patagonia as far as the genetic influence of *T. m. vanvolxemii* extends, i.e. the Gulf of San Jorge. The S limits of *Colias lesbia* (as an occasional seasonal breeder) and *Eurema deva* (as an immigrant) are in the same area. It would be instructive to use Satyrids to define the limits in these same areas, as they are grassland-associated while the Pierids are not necessarily so.

Quaternary Climate Dynamics and Dispersal Routes. During the Quaternary the extreme aridity which characterizes the coastal deserts of Peru and northern Chile developed, serving as a very effective barrier to contain the biota of the Andean highlands. At the same time, there is reason to believe that precipitation waxed and waned repeatedly in temperate Chile, resulting in pulsations of N-ward migration by the Valdivian rain forest. Relict elements of that forest exist today in such areas as Fray Jorge, Talinay and Mantagua in Coquimbo at roughly 30°S, near the N limits of many organisms of central Chile including the butterflies *Tatochila mercedis* and *Colias vauthierii.* The best butterfly indicator of the Valdivian forest, *Eroessa chiliensis*, seems to stop at about 35°S (Constitución). Caviedes (1990) provided a predictive model of precipitation which generates up to 9-fold increases in rainfall in central Chile with T depressions of 3°C or less. If these calculations are valid, the gradient between the desertic Atacama climate and the much wetter central Chilean climate must have been extremely steep at times in the Quaternary (Paskoff, 1977). Caviedes and Iriarte (1989) have used these projections to develop a verbal model which accounts for the distribution of faunal richness of Cricetid rodents and possibly other mammals in Chile and Argentina. They conclude that the Atacama barrier would have held in the rich, diverse and highly endemic Cricetid faunas (cf. Pierini), forcing whatever dispersal occurred to have been down the eastern (Argentine) side of the mountains in the relatively mesic climates influenced by the tropical flow from the NE. During the periodic episodes when Valdivian vegetation migrated N-ward to the vicinity of 30° in Chile, many of the trans-Andean passes would have been available for faunal migration from E to W. The limited Chilean fauna S of the Atacama can be derived from such movements.

Cricetids resemble butterflies in having greater faunal richness on average E of the Andes, but the resemblances break down on detailed examination. Pierids (except *Eroessa* and *Mathania*) are not forest species and indeed would be excluded from extensively-forested areas. There is no Pierid fauna in archipelagic Chile, and little butterfly fauna at all. The same phenomenon can be seen in the North American Pacific NW rainy belt. For the Cricetid model to account for the Patagonian character of the Chilean Central Valley fauna, the necessary assemblage would have to have been far enough N on the Argentine side to have crossed the passes between 33–30°S (including the Bermejo) when they were sufficiently mesic to be good corridors. There is no concrete evidence bearing on this. See also Heusser, 1983 and Veblen *et al.* 1981.

What we do know of butterflies crossing the Andes is based largely on the passes in the Lake District, which today are mesic and penetrable but were icebound in the Pleistocene. All the movement we can detect has been from W to E in these passes, following climate and prevailing winds. Thus, the hybrid-zone phenomena described for *Tatochila mercedis* and *autodice* are presumably post-Pleistocene in origin. It is striking, however, that populations of *T. m. vanvolxemii* from further N (Copahue and Paso Bermejo-Potrerillos) show signs of previous gene flow from nominate *mercedis* over the crest, though the genitalic morphology that defines such contacts farther S has disappeared. This presupposes the existence of *mercedis* in Chile at least during one fairly recent more mesic interval, and thus implies latitudinal oscillation of ranges. The stranded high-Andean taxa in the Cordón del Viento imply a retreat N-ward with recent drying, as do the ranges of the high-altitude taxa in Salta, Jujuy and Tucumán. (Cei, 1980 discusses some possible biogeographic roles of the *yungas* in the Quaternary.)

"The Argentine provinces of Mendoza and San Juan report 2.5 times as many mammal species as the Chilean provinces at equivalent latitudes" (Caviedes and Iriarte 1989). These provinces are, however, very depauperate insofar as Pierid butterflies are concerned. Although both the timing of S-ward movement and the general routes of dispersal may be similar for Pierids and Cricetids, it is still necessary to account for such striking contradictions in their distributions.

Perspectives on Faunistics. Hayward (1955c) noted that high-Andean elements penetrated the *cuyo* in the Uspallata Valley. Despite the unusually clear overall phytogeographic patterns defined by climate, any attempt to define precise boundaries for the Argentine floras and faunas is bound to be frustrated by the individualistic nature of species distributions. Both the high-Andean and Patagonian floras show abundant evidence of relative youth and evolutionary dynamism, while the Valdivian forest is clearly relictual and ancient. The butterfly faunas treated in this paper have little connection to the Valdivian forest (except *Eroessa chiliensis*), and no butterfly in the region — Pierid or otherwise — is tied by identified sister-group relationships to any other austral region so as to suggest a Gondwanaland-based history. The nearest relative of *Eroessa* is by no means clear. Klots (1932) correctly identifies it as exceedingly primitive in genitalia, venation and form of palpus. Electrophoretically it comes closest to the east-Asian and Indian genus *Hebomoia* Hbn., which shares one probable apomorphic trait with *Hesperocharis* Felder (including *Mathania*); few taxa have been examined in this group of genera (Geiger and Shapiro, unpublished). There are, however, a variety of suggestive trans-Pacific linkages in Pieridae, which if substantiated would imply considerably greater antiquity for the modern butterflies than has been established in the fossil record; these will be discussed elsewhere.

The traditional geochronology of the Andes has the cold-adapted high-altitude biota, which shows a dominance of circumboreal taxa at the family level (Van der Hammen and Cleef 1987, Raven and Axelrod 1974), entering late in the Pliocene when the latest uplift reached adequate heights to support such a biota. By this view, these organisms have undergone extensive adaptive radiation since the initial phases of the Great American Interchange (Stehli and Webb 1985). It is increasingly clear that this scenario is too simple, and probably largely wrong. More groups have been shown in the fossil record to have arrived in South America from elsewhere before the Interchange, and, more importantly, the amount of differentiation in some high-Andean groups appears too great to be accommodated in so little time. This very large literature is summarized by Briggs (1987), who emphasizes the complexity of patterns observed in different taxonomic groups and their inferred differential antiquity on the continent. The various genera of Andean pierines seem unlikely to have originated and diversified within only 2 or 3 MY — especially since our estimates of the antiquity of *speciation* based on electrophoretic differences tend to fall close to that number (Geiger and Shapiro, unpublished; compare Shapiro and Geiger, 1989 for *Vanessa* across the Isthmus of Panama). But how could cold-adapted genera antedate cold environments? It is of course possible that they arrived on the suggested schedule, but already generically differentiated elsewhere. This requires multiple colonizations by small and weak-flying animals over very great distances. Given the strong morphological affinities to the Asiatic alpine genus *Baltia* Moore, affinities which appear real and not convergent (Field 1958, though the electrophoretic data, such as they are, are ambiguous — Geiger, Michel and Shapiro, unpublished data), some kind of Matthew (1915) "Camelid scenario" appears required. By this view the Asiatic and South American genera were linked across North America and might even have originated there, but subsequently went extinct there. We are unlikely to get fossils to vindicate this scenario, as they have for the Camelidae. But recent evidence (Mercer and Sutter 1982, Clapperton 1983) strongly suggests that Patagonia underwent episodes of glaciation some 7 and 4.6 MYA, before the Ice Ages began in the N Hemisphere (except perhaps in Alaska). This lengthens the potential time-line for the evolution of adaptation to cold in South America, without clarifying the question of where the Pierini came from or who their ancestors might have been.

The genus *Tatochila* is apparently evolving very rapidly right now throughout the Andes, with all sorts of speciation-related phenomena visible, a "ferment of variability" as Dunbar (1968) described the situation in Arctic crustaceans. For a North American butterfly worker it is strikingly reminiscent of the situation in the *machaon* L. group of *Papilio* — the entities are often not fully speciated, intergrade in complex ways, form hybrid zones, produce local subspecies in some areas and not others, and in general look like sequelae of the Pleistocene (compare Sperling 1987). The data for *Hypsochila* are only beginning to accumulate, but clearly suggest a group in similar if less extensive ferment. The *Phulia* group of taxa are perplexing in that morphospecies tend to appear older than in *Tatochila*, but local populations of the *Phulia nymphula* complex are clearly evolving in a variety of directions, and the various *Infraphulia* and *Pierphulia* look similar. For all these taxa, the genera and subgenera certainly antedate the Pleistocene, speciation may often also, but subspeciation seems to have been working overtime in the Quaternary.[5]

The ultimate interpretation of these radiations will depend on our ability to develop a convincing reconstruction of pierine phylogeny and to determine whence came the stem-species of the various radiations. At present we can say reasonably confidently that *Tatochila*, in its current broad sense, has undergone several radiations, all of which may still be in progress. Certainly the two southernmost (*mercedis* and *theodice*) are, and the next southernmost (*autodice*) is clearly quite active too. The central-Andean/*yungas* taxa are so beset with taxonomic problems that we may infer activity there too, even if we do not understand it. In the far N, *T. xanthodice* Lucas is actively differentiating in different ranges (Ackery 1975). Although we are still not in a position to interpret the extreme rarefaction of the Andean pierines in the N, we can say it is not *de facto* evidence of Gondwanaland origins for the group. Rather, it suggests spread both N and S from a central-Andean center for several genera, though that "center" may not be where they *originated.*

The Fuegian and far-S Patagonian taxa range from the probable ancient relict *Colias ponteni*, to recently-derived and still only weakly-differentiated subspecies in *Tatochila* which as noted above may antedate the inundation of the Straits of Magellan, but perhaps not by much. The mere fact of remoteness in far-southern South America may have preserved *Colias ponteni* and *Eroessa chiliensis* — which once may have ranged much more widely, and may indeed have originated elsewhere.

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[5] The maximum antiquity of *T. m. vanvolxemii* and other taxa of the *monte* can be inferred from recent discussions of the evolution of aridity in Argentina. Volkheimer (1971) inferred humid climates in Patagonia except perhaps semiarid in the modern *pampa* region in the early Tertiary, and again in the Miocene. Axelrod (1979) and Sarmiento (1975) both consider the *monte* and the Patagonian steppe as consequences of the Plio-Pleistocene elevation of the Andes, disagreeing with Solbrig (1976), who feels that arid climates might have existed longer. Since *vanvolxemii* is highly derivative vis-à-vis its relatives, it almost certainly has originated within this time frame. Axelrod (*loc. cit.*) accepts the spotty evidence from Bolivia of an emerging xerophytic-microphyllous vegetation there perhaps as early as the late Eocene, but in any case well-defined by the Miocene. The *Phulias* could thus conceivably go back that far, but whence came their ancestors?

Biogeographers tend to believe what geoscientists tell them about the antiquity of continents and orogenies, a dangerous tendency (though some biogeographers championed continental drift when the geoscientists mainly considered it impossible). In interpreting the distributions and phylogenies of Andean organisms we have always attempted to ram everything into the short time since the late Pliocene, because geoscientists said we had to. Now some glaciologists (Clapperton, Mercer) hold out the possibility of a considerably longer time-line (at least 4, perhaps 6 or 7 million years). Just what this implies for us is still unclear. Nothing in the butterfly data yet *requires* a longer Andean time-line; thanks to the *Baltia* connection we can always make up stories about generic differentiation having occurred elsewhere. And it is clear that much of the evolutionary activity in the Andean-Patagonian Pieridae *is* very young, certainly of Holocene origin. Table 4 summarizes what we might know at the moment, which in terms of data is far greater than what Giacomelli (1915) knew when he published his concluding table, yet not much more definitive!

There is one further approach to these problems, which has not been addressed here. It is strictly ecological and ahistorical and in the "MacArthur tradition," exemplified by the analysis of the Argentine passerine bird fauna by Rabinovich and Rapoport (1975). Neither the size of the Pierid fauna nor the completeness of ground coverage justifies such an analysis at this time. It may ultimately be useful, but it should be obvious that such an approach ignores many of the most interesting and evolutionarily exciting phenomena of faunistics.

Now that we have learned a little more, we can join Giacomelli in lamenting the profundity of our ignorance. Giacomelli wrote even as his compatriots Florentino Ameghino and Francisco P. Moreno were beginning the process of opening up the inescapably complicated geohistorical context in which the Argentine Pierid fauna is imbedded. The ultimate fruits of their labor can be seen in the informed nature of our modern, profound uncertainty.

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	Puna de Atacama (Chile)	Puna de Jujuy/Salta	Cuesta del Obispo/Co.Zapallar	Sierras Pampeanas	Arroyo de Agua Negra	Paso Bermejo	Cordon del Cepo	Precordillera Chilena	Valle Central (Chile)	Precordillera Mendocina	Valles Calchaquies	Cordon del Viento	Chos Malal	Loncopue	Alumine	San Martin - P.N. Lanin	Bariloche - P.N. Nahuel Huapi	Esquel - P.N. Los Alerces	Laguna del Maule	Comodoro Rivadavia - Fitz Roy	Valdivia Region	Rio Gallegos	Rio Grande	Ushuaia - Cordon Martial	Chilean Magallanes
I. ilyodes	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. r. rosea	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. r. maria	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. isabela	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. nymphula	X	X	X	X	X	X	X	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0
H. penai	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. w. sulfurodice	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. w. wagenknechti	0	0	0	0	X	X	X	0	0	0	0	0	0	0	0	X	0	0	X	0	0	0	0	0	0
H. galactodice	0	X	0	0	0	0	0	0	0	0	0	X	0	X	X	0	X	X	0	0	0	0	0	0	0
H. huemul	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	X	0	0	0	0	0	0
H. microdice	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	X	X
H. argyrodice	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	X	X	X
T. t. theodice	0	0	0	0	0	0	0	X	0	0	0	0	0	X	X	X	X	0	X	0	X	0	0	0	0
T. t. gymnodice	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	X
T. t. staudingeri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	X
T. a. autodice	0	0	0	0	0	0	0	0	0	X	X	X	X	X	0	X	X	X	0	X	0	0	0	0	0
T. a. blanchardii	0	0	0	0	0	0	X	X	X	0	0	0	0	0	X	X	X	X	X	0	0	0	0	0	0
T. a. ernestae	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T. m. mercedis	0	0	0	0	0	0	X	X	X	0	0	0	0	0	X	X	0	0	X	0	X	0	0	0	0
T. m. macrodice	X	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T. m. vanvolxemii	0	0	0	0	0	0	0	0	0	X	X	0	X	X	0	0	0	0	0	X	0	0	0	0	0
T. m. sterodice	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	X	X	X	0	0	0	X	0	0	X
T. m. fueguensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	X	X
T. inversa	0	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T. orthodice	0	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T. stigmadice	0	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T. mariae	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T. d. distincta	0	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T. d. fieldi	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E. chilensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	0	0	0	X	0	0	0	0
M. leucothea	0	0	0	0	0	0	0	X	0	0	0	0	0	0	0	X	X	0	0	0	X	0	0	0	0
C. lesbia	X	X	X	X	0	0	0	0	0	X	X	X	X	X	X	0	X	0	0	X	0	0	0	0	0
C. weberbaueri	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C. blameyi	0	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C. flaveola	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C. vauthieri	0	0	0	0	0	0	X	X	X	0	0	0	X	X	X	X	X	X	X	X	X	X	0	0	X
C. ponteni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X
F. deva	X	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	X	0	0	0	0	0
T. riojana	X	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
# of species:	15	12	10	10	3	2	5	5	3	3	3	4	4	7	7	10	10	5	6	6	5	4	5	4	8

Table 1. Occurrence of selected pierine species in selected areas of Argentina and Chile.
Colias mendozina from the Paso Bermejo is omitted from this and subsequent analyses.

	Puna de Atacama (Chile)	Puna de Jujuy/Salta	Cuesta del Obispo/Co.Zapallar	Sierras Pampeanas	Arroyo de Agua Negra	Paso Bermejo	Cordon del Cepo	Precordillera Chilena	Valle Central (Chile)	Precordillera Mendocina	Valles Calchaquies	Cordon del Viento	Chos Malal	Loncopue	Alumine	San Martin - P.N. Lanin	Bariloche - P.N. Nahuel Huapi	Esquel - P.N. Los Alerces	Laguna del Maule	Comodoro Rivadavia - Fitz Roy	Valdivia Region	Rio Gallegos	Rio Grande	Ushuaia - Cordon Martial	Chilean Magallanes
Puna de Atacama	X	6	5	5	1	1	1	0	0	1	1	2	1	1	1	0	1	0	0	1	0	0	0	0	0
Puna de Jujuy/Salta		X	10	10	1	1	1	0	0	1	1	3	1	2	2	0	2	1	0	1	0	0	0	0	0
Cuesta del Obispo			X	10	1	1	1	0	0	1	1	2	1	1	1	0	1	0	0	1	0	0	0	0	0
Sierras Pampeanas				X	1	1	1	0	0	1	1	2	1	1	1	0	1	0	0	1	0	0	0	0	0
Arroyo de Agua Negra					X	2	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Paso Bermejo						X	2	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Cordon del Cepo							X	3	3	0	0	1	1	1	3	4	3	3	2	1	1	1	1	0	1
Precordillera Chilena								X	3	0	0	0	1	2	4	5	4	4	2	1	3	1	0	0	1
Valle Central (Chile)									X	0	0	0	3	1	3	3	2	2	3	1	2	1	0	0	1
Precordillera Mendocina										X	3	2	3	3	1	1	2	1	0	3	0	0	0	0	0
Valles Calchaquies											X	2	3	3	1	1	2	2	0	3	0	0	0	0	0
Cordon del Viento												X	2	3	3	1	3	2	0	2	0	0	0	0	0
Chos Malal													X	4	2	2	2	3	1	4	2	1	0	0	1
Loncopue														X	5	4	4	4	2	4	2	2	1	0	2
Alumine															X	5	6	4	4	2	3	2	1	0	2
San Martin de los Andes - Parque Nacional Lanin																X	7	4	5	2	5	2	1	0	2
San Carlos de Bariloche - Parque Nacional Nahuel Huapi																	X	5	3	4	4	2	0	0	2
Esquel - Parque Nacional Los Alerces																		X	2	2	1	2	0	0	2
Laguna del Maule																			X	1	3	1	0	0	1
Comodoro Rivadavia - Fitz Roy																				X	1	0	1	0	2
Valdivia Region																					X	1	0	0	4
Rio Gallegos																						X	2	2	4
Rio Grande																							X	2	2
Ushuaia - Cordon Martial																								X	4
Chilean Magallanes																									X

Table 2. Numbers of species shared by all possible pairs of regions. Data from table 1.

Puna de Atacama (Chile)	Puna de Jujuy/Salta	Cuesta del Obispo/Co.Zapallar	Sierras Pampeanas	Arroyo de Agua Negra	Paso Bermejo	Cordón del Cepo	Precordillera Chilena	Valle Central (Chile)	Precordillera Mendocina	Valles Calchaquíes	Cordón del Viento	Chos Malal	Loncopué	Aluminé	San Martín - P.N. Lanín	Bariloche - P.N. Nahuel Huapí	Esquel - P.N. Los Alerces	Laguna del Maule	Comodoro Rivadavia - Fitz Roy	Valdivia Region	Río Gallegos	Río Grande	Ushuaia - Cordón Martial	Chilean Magallanes	
+	.286	.250	.250	.059	.063	.053	.000	.000	.059	.059	.118	.056	.048	.048	.000	.042	.000	.000	.050	.000	.000	.000	.000	.000	Puna de Atacama (Chile)
	+	.833	.833	.071	.077	.063	.000	.000	.071	.071	.230	.067	.118	.118	.000	.100	.063	.000	.059	.000	.000	.000	.000	.000	Puna de Jujuy/Salta
		+	1.000	.083	.091	.071	.000	.000	.083	.083	.167	.077	.063	.063	.000	.053	.000	.000	.067	.000	.000	.000	.000	.000	Cuesta del Obispo/Co.Zapallar
			+	.083	.091	.071	.000	.000	.083	.083	.167	.077	.063	.063	.000	.053	.000	.000	.067	.000	.000	.000	.000	.000	Sierras Pampeanas
				+	.500	.333	.000	.000	.000	.000	.167	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	Arroyo de Agua Negra
					+	.667	.000	.250	.000	.000	.200	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	Paso Bermejo
						+	.429	.600	.000	.000	.125	.125	.091	.333	.364	.250	.430	.222	.100	.111	.125	.111	.000	.083	Cordón del Cepo
							+	.600	.000	.000	.000	.125	.200	.500	.500	.364	.667	.222	.100	.430	.125	.000	.000	.083	Precordillera Chilena
								+	.000	.000	.000	.750	.111	.429	.300	.182	.286	.500	.125	.333	.167	.000	.000	.100	Valle Central (Chile)
									+	1.000	.400	.750	.429	.111	.083	.182	.333	.000	.500	.000	.000	.000	.000	.000	Precordillera Mendocina
										+	.400	.750	.429	.111	.083	.182	.333	.000	.500	.000	.000	.000	.000	.000	Valles Calchaquíes
											+	.333	.375	.375	.077	.273	.286	.000	.250	.000	.000	.000	.000	.000	Cordón del Viento
												+	.571	.222	.167	.167	.500	.111	.667	.286	.143	.000	.000	.091	Chos Malal
													+	.556	.308	.308	.500	.182	.444	.200	.200	.091	.000	.154	Loncopué
														+	.417	.545	.500	.444	.182	.333	.222	.091	.000	.154	Aluminé
															+	.539	.364	.455	.143	.500	.167	.072	.000	.125	San Martín - P.N. Lanín
																+	.500	.231	.333	.364	.167	.000	.000	.125	Bariloche - P.N. Nahuel Huapí
																	+	.222	.222	.111	.286	.000	.000	.182	Esquel - P.N. Los Alerces
																		+	.091	.375	.111	.000	.000	.077	Laguna del Maule
																			+	.100	.000	.100	.000	.167	Comodoro Rivadavia - Fitz Roy
																				+	.125	.000	.000	.444	Valdivia Region
																					+	.286	.333	.500	Río Gallegos
																						+	.286	.182	Río Grande
																							+	.500	Ushuaia - Cordón Martial
																								+	Chilean Magallanes

Table 3. Sørensen's index of similarity used to compare all possible pairs of faunas from Table 2. These data are presented as a dendrogram in Fig. 23.

EPOCH	TIME	GEOHISTORY	BIOTA	PIERIDAE
HOLOCENE	0–1 KYA	*Glaciers retreating in Mendoza and Tucumán; much fluctuation in glacial advances and retreats in Patagonia*		W–>E Cross-Andean migrations in NW Patagonia; origin of hybrid zones in *Tatochila*; weak subspeciation in NW *Tatochila* taxa
	10	*warm interval*	Strandings in Cordón del Viento; High Andean fauna in NW assumes present configuration	
		Deglaciation of Fuego-Patagonian lowland commences	Colonization of Fuegia from Patagonian mainland	
	20	***ULTIMATE MAJOR GLACIATION***	Patagonian faunal refugia along coastline and on continental shelf; Andean fauna in NW shifted downslope	
	30			
PLEISTOCENE	MYA	***PENULTIMATE GLACIATION 0.13-0.17 MYA***		
	0.5			
	1.0	***GREATEST PATAGONIAN GLACIATION*** *(Condor Cliff—Initioglacial—Pichi Leufu)*	Repeated N-S biotic migrations on both sides of cordillera	E–>W cross-Andean migrations into Chile at latitude of Mendoza & San Juan; subspecific differentiation in *Tatochila mercedis* complex?
	1.5		Origin of Atacama desert barrier to dispersal; origin of Argentine *monte* desert	Origins of Andean Pierine species?
	0–2.2	***FREQUENT PATAGONIAN GLACIATIONS***		
PLIOCENE	2.0	*Usual assumed earliest date of Andean uplift to alpine heights*		
	2.5	*(First buildup of mid-latitude Northern hemisphere ice sheets)*		
	3.0			Origins of Andean Pierine genera?
	3.5	*First "definite" Patagonian glaciation; inference (Clapperton) that Andes already near present heights*		
	4.0			
	2.2–4.5	***PRE-PLEISTOCENE TILLS IMPLY GLACIATIONS POSSIBLY BACK TO 7 MYA; NO DIRECT EVIDENCE***		
	4.5			
		Beginning of ancestral Andean orogeny Paleocene — Eocene	First evidence of Bolivian altiplano vegetation in Miocene (or perhaps Eocene?)	

Table 4. Attempted cross-correlation of geohistorical and biotic events in the southern Andes and Patagonia with development of the Pierid butterfly fauna. KYA = thousands of years ago; MYA = millions of years ago. Note discrepancy between the usual Plio-Pleistocene estimate for the origin of alpine habitats in the Andes and the much older estimate inferred by Mercer and Clapperton from alleged pre-Pleistocene tills, and the older-still earliest paleobotanical evidence for xerophytic vegetation in Bolivia. Very detailed paleoclimatic sequences are available for the Holocene in much of southern South America, but the quality and quantity of evidence diminish with time. Pre-Pleistocene events are in part inferred by cross-correlation with evidence bearing on marine temperatures near New Zealand (see Clapperton reference).

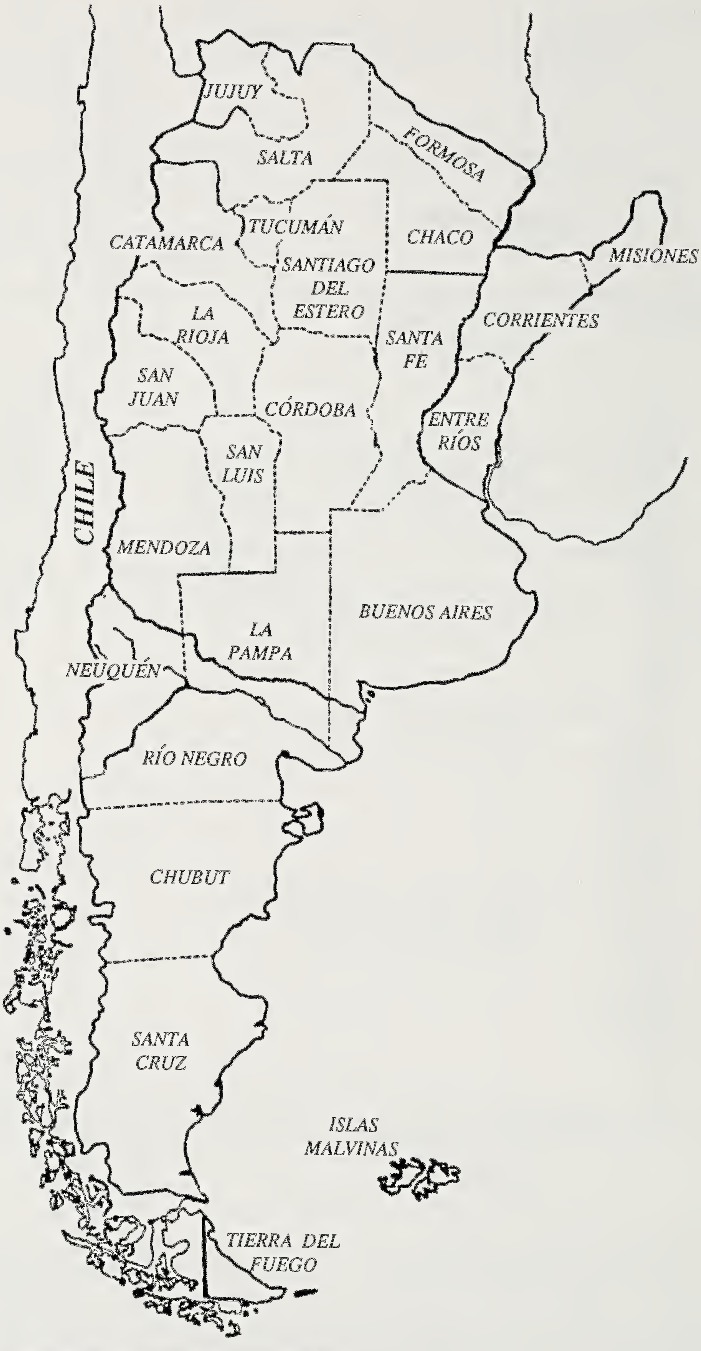


Fig. 1. Political map of Argentina.

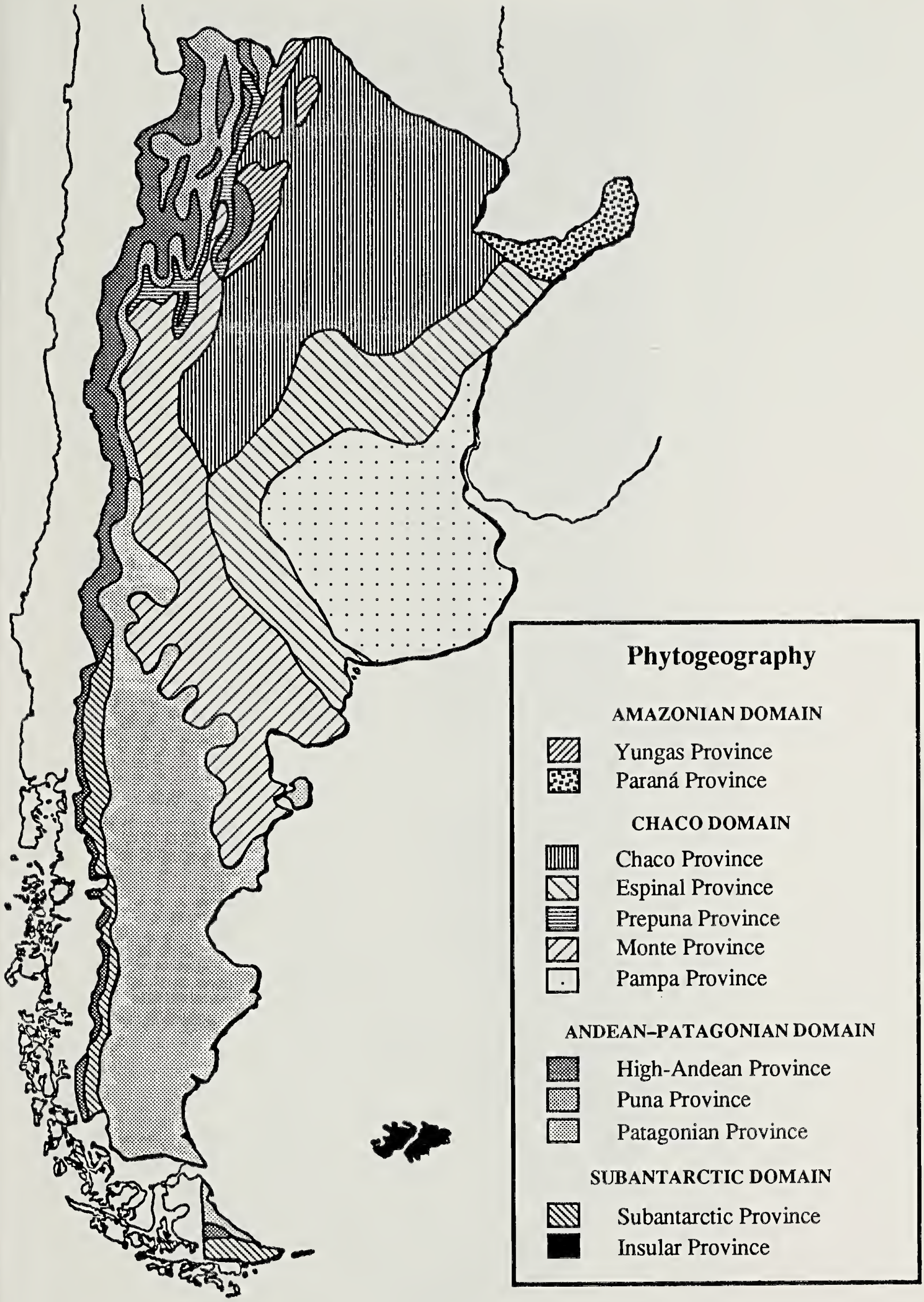


Fig. 2. Phytogeography of Argentina, redrawn from Cabrera, 1971. Fig. 1.

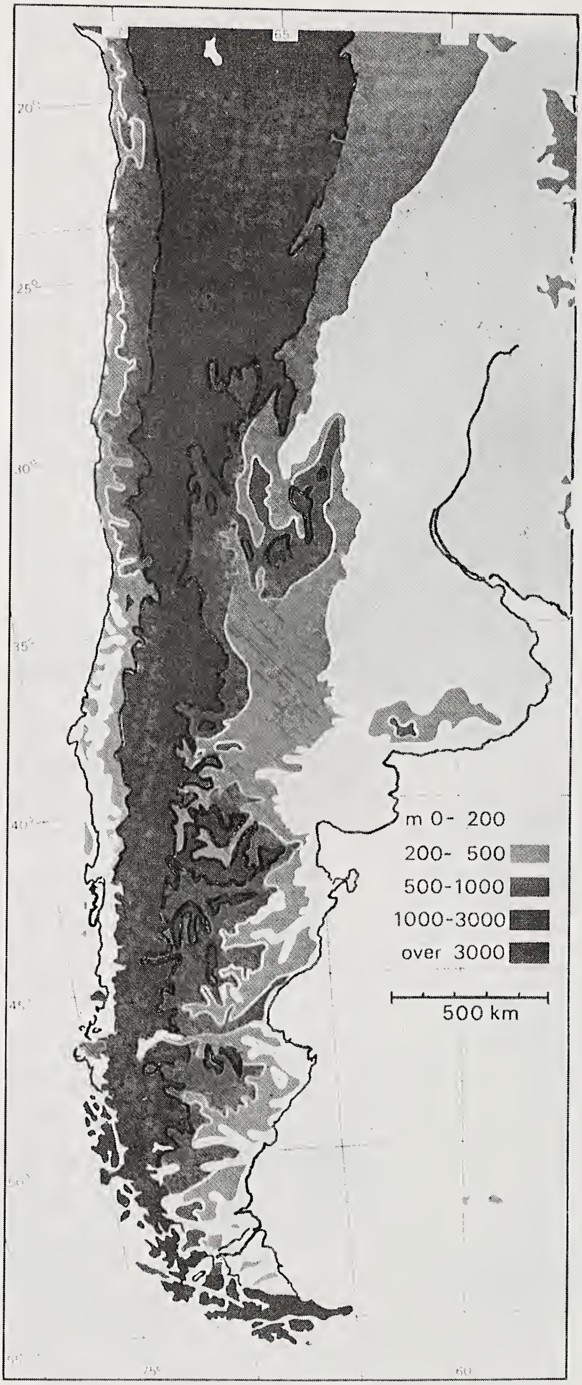


Fig. 3. Distribution of altitude above sea level in Argentina and Chile, from Madsen *et al.*, 1980.

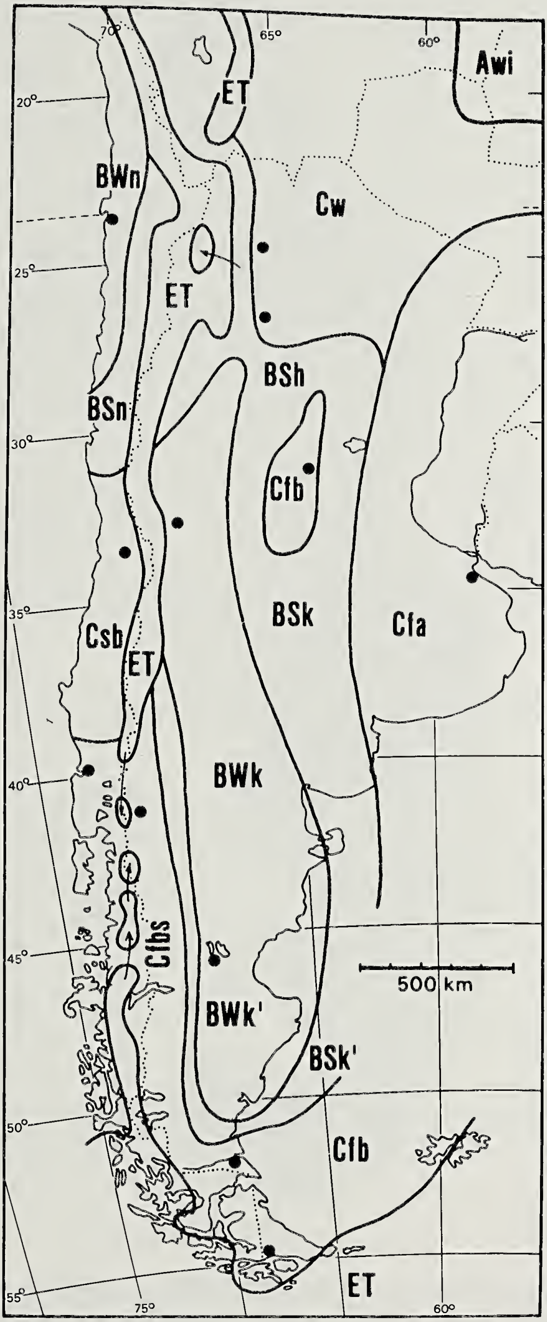


Fig. 4. Climate types of Argentina and Chile according to the Köppen system, from Madsen *et al.*, 1980.

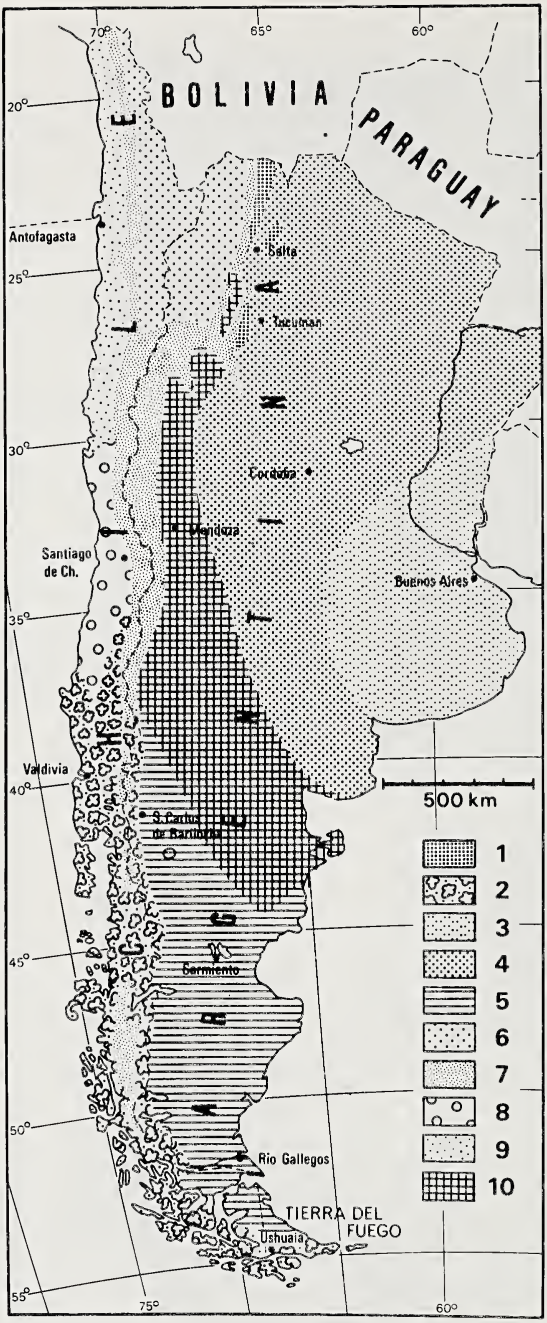


Fig. 5. Phytogeography of Argentina and Chile as mapped by Madsen *et al.*, 1980. Key: 1. Subtropical forest; 2. Subantarctic (mostly *Nothofagus*) forest; 3. Pampa; 4. Xerophytic woodland and scrub (Espinal); 5. Patagonian steppe; 6. Puna; 7. Andean boreal and nival zones; 8. Chilean Mediterranean scrub (Matorral) and valley grassland; 9. Atacama Desert; 10. Monte Desert and arid montane (Prepuna). Compare Fig. 2.

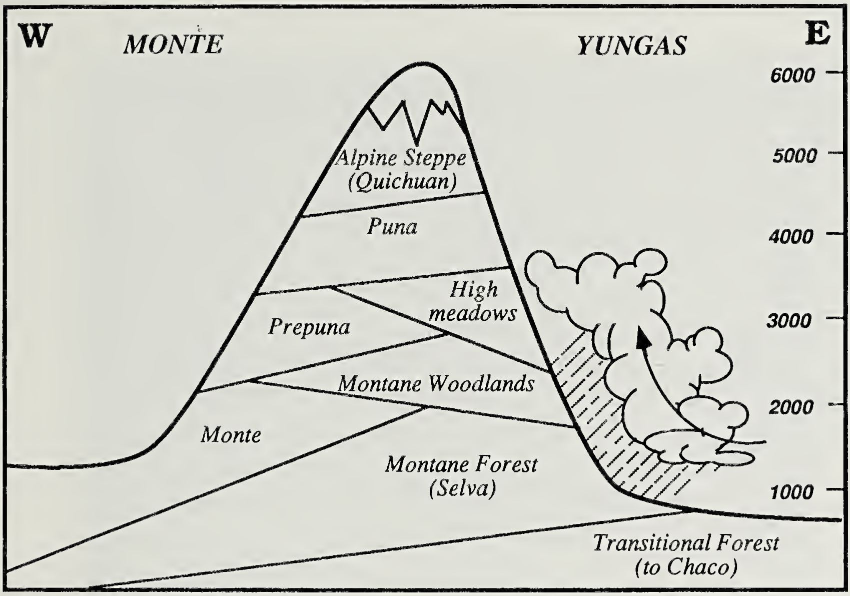


Fig. 6. Generalized distribution of vegetation types in NW Argentina, reflecting orographic influences on precipitation. Redrawn from Cabrera, 1971.

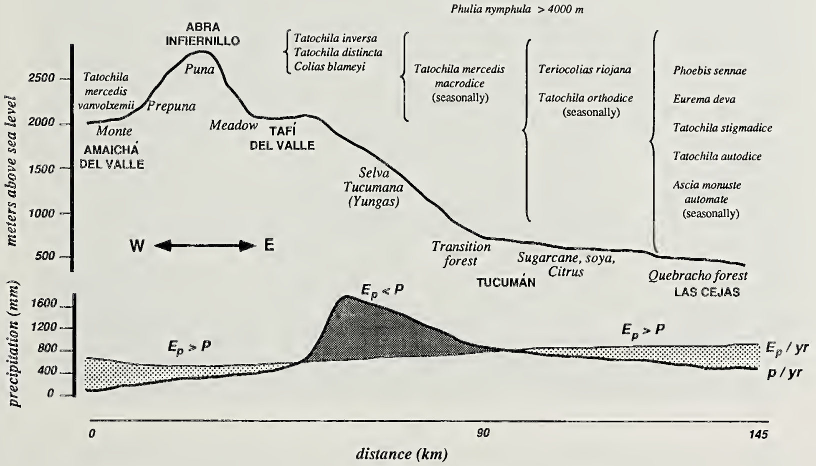


Fig. 7. Transect across the *Sierras Pampeanas* in Tucumán, showing vegetation types, altitudinal distribution of Pieridae, and relationship of Precipitation (P) to Potential Evapotranspiration (E_p) (annualized). *Phulia nymphula* occurs only on the peaks over 4000 m, not reaching the level of Abra Infiernillo. Partially redrawn after Madsen *et al.* (1980).

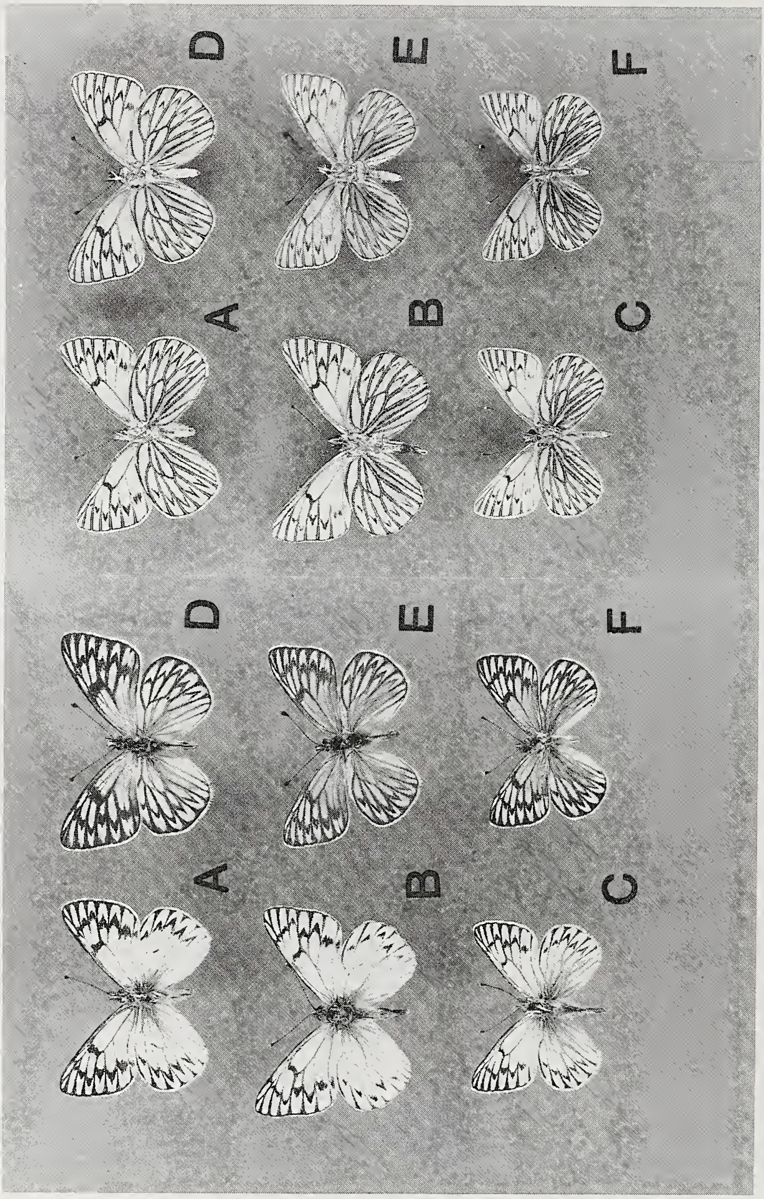


Fig. 8. *Tatochila theodice* along a latitudinal cline. A–C, males; D–F, females. A, Loncopué, Neuquén, 8.XI.1988 (first brood) (N-most known population of nominate *theodice* in Argentina). B, La Esperanza, Santa Cruz, 15.I.1979 (DE) (2nd brood) (± *gymnodice*). C, Río Grande, Tierra del Fuego, 25.XI.1988 (1st brood) (± *staudingeri*). D, Puerto Blest, Parque Nacional Nahuel Huapí, Río Negro, 28.II.1979 (DE) (2nd brood?) (*theodice*). E, Lago Argentino, Santa Cruz, 11.I.1979 (DE) (2nd brood?) (± *gymnodice*). F, Río Grande, Tierra del Fuego, 25.XI.1988 (1st brood) (± *staudingeri*).

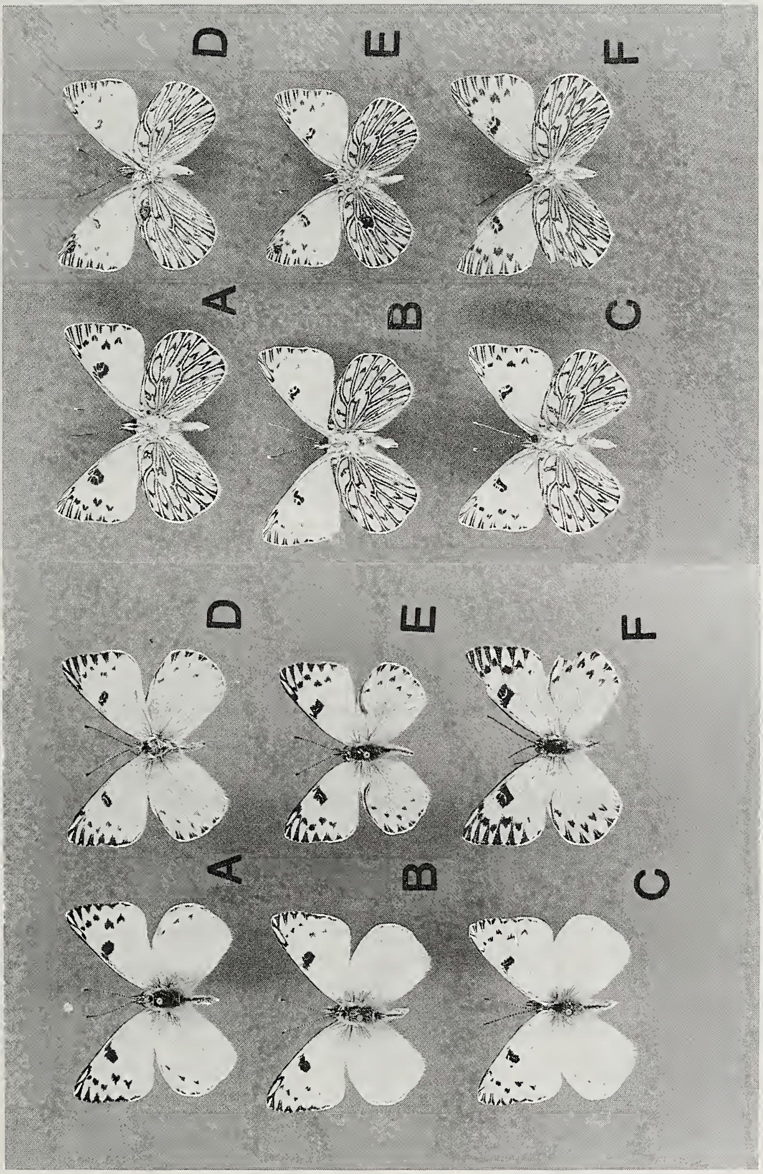
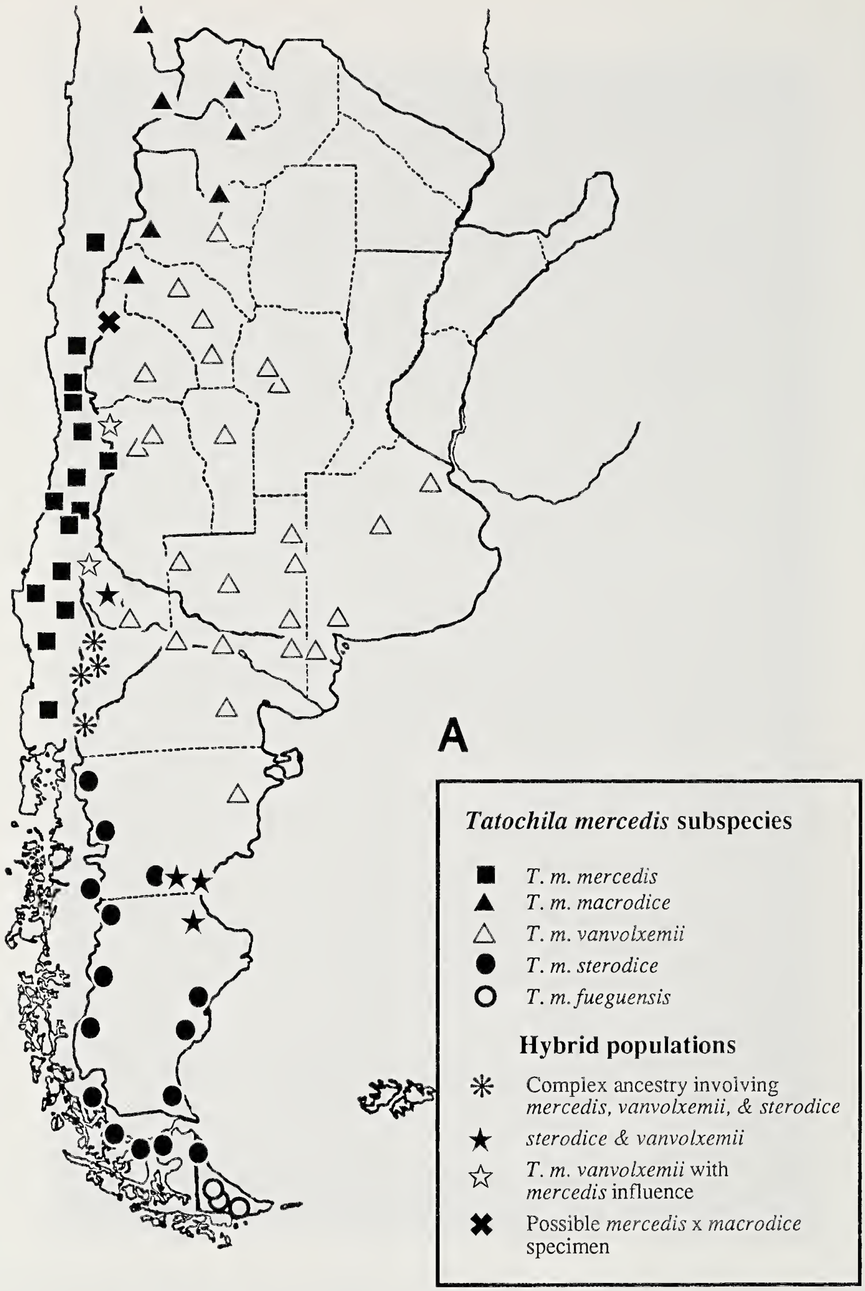
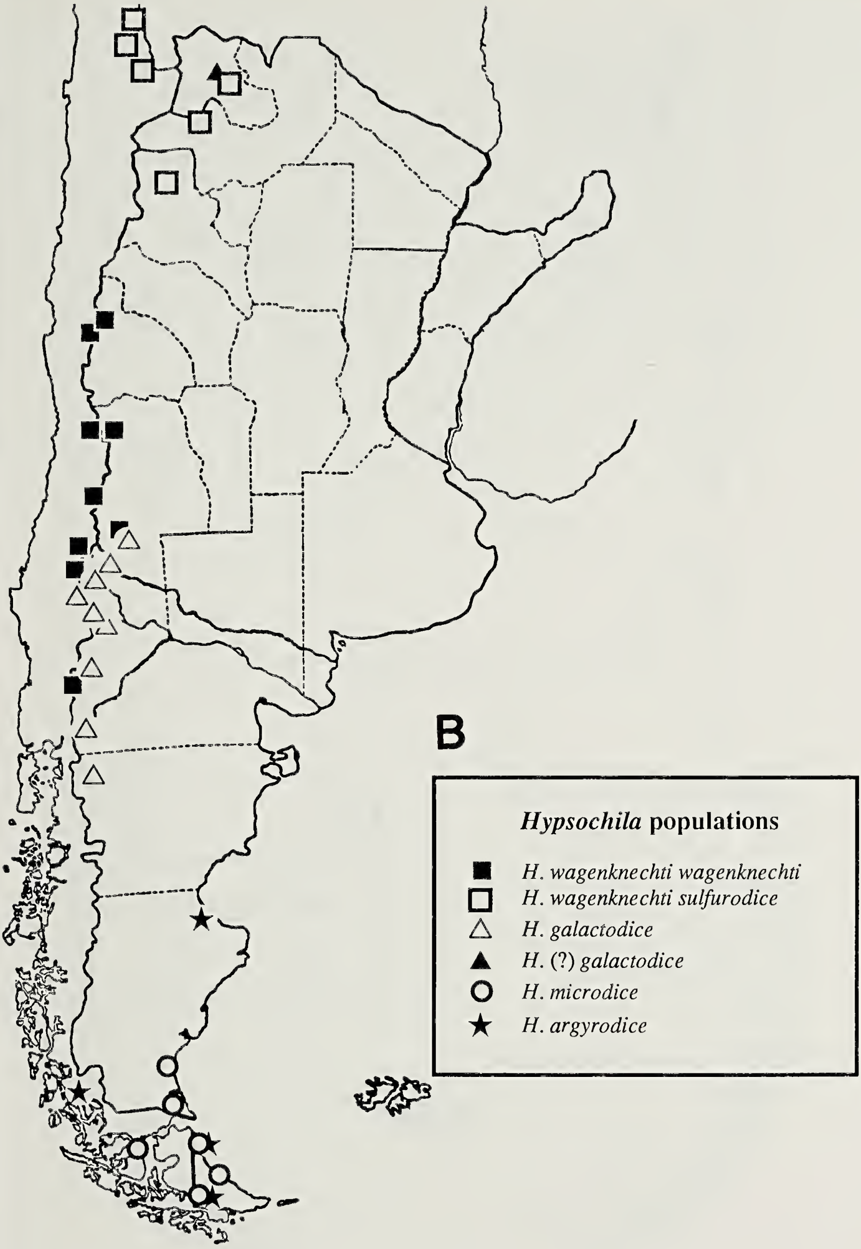
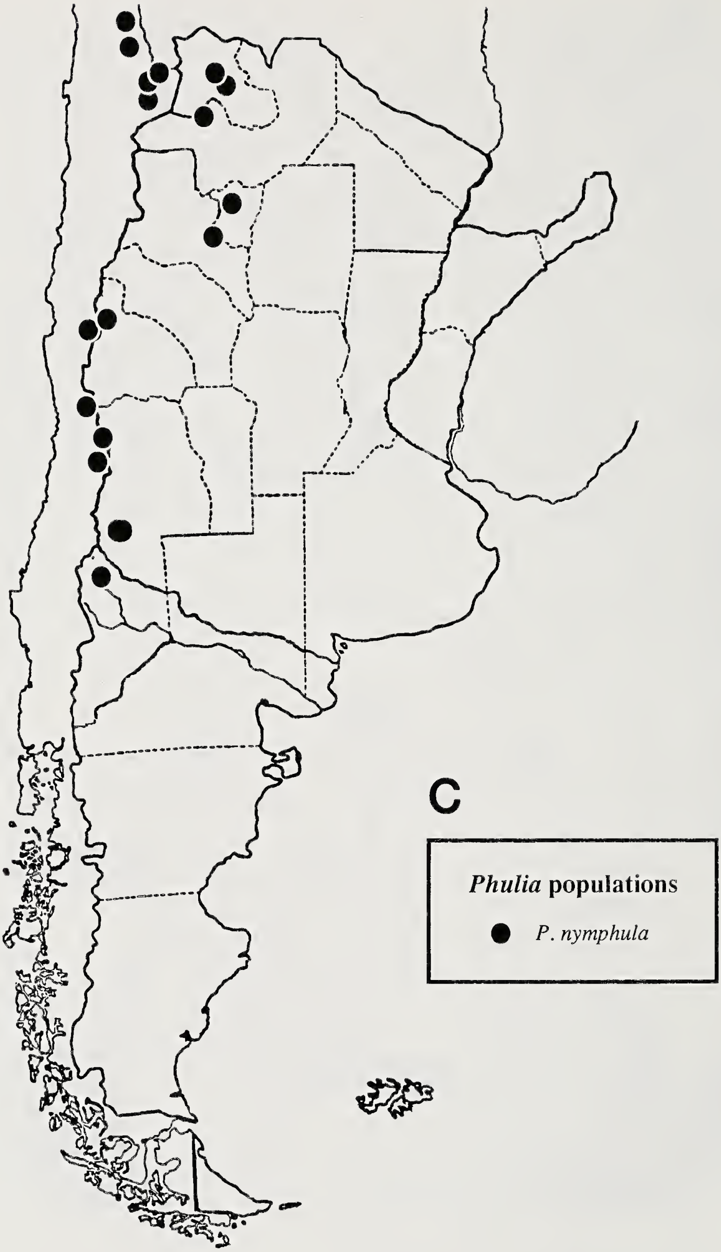


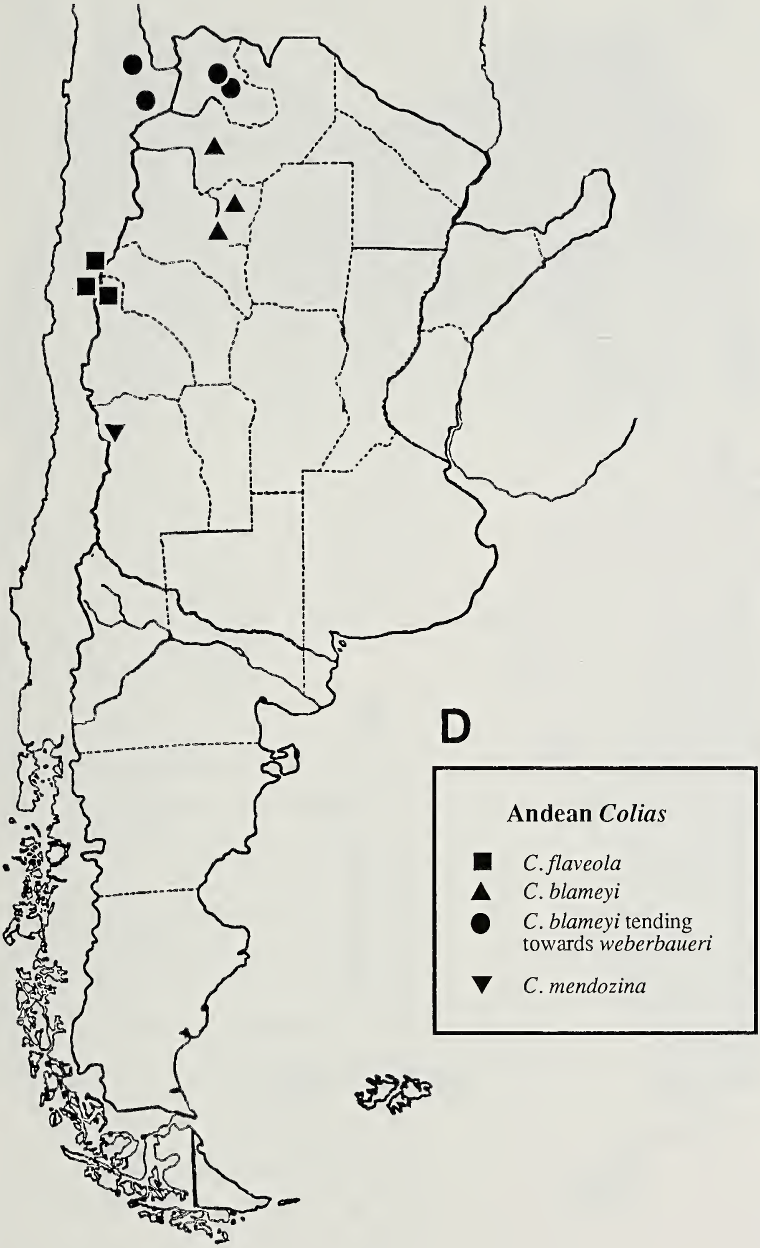
Fig. 9. *Tatochila autodice — blanchardii* intergrades reared from wild ova collected in the NW Patagonian hybrid zone, XI.1988. A–C, males; D–F, females. A, D, E from Esquel, Chubut; B, C, F from San Carlos de Bariloche, Río Negro. Specimens A and F are within the range of variation of pure Chilean *blanchardii*. See Shapiro, 1986a for characters.


A
Tatochila mercedis subspecies
■ T. m. mercedis
▲ T. m. macrodice
△ T. m. vanvolxemii
● T. m. sterodice
○ T. m. fueguensis
Hybrid populations
✳ Complex ancestry involving mercedis, vanvolxemii, & sterodice
★ sterodice & vanvolxemii
☆ T. m. vanvolxemii with mercedis influence
✖ Possible mercedis x macrodice specimen

Figs. 10A–D. Distributions of selected taxa, superimposed on political map of Argentina. A: *Tatochila mercedis* subspecies. B: *Hypsochila*, except *H. penai* and *H. huemul*, for which no new data are reported. C: *Phulia nymphula*. D: Andean *Colias*. Chilean data mostly from Field and Herrera, Herrera and Field, and Herrera references in text.


B
Hypsochila populations
■ *H. wagenknechti wagenknechti*
□ *H. wagenknechti sulfurodice*
△ *H. galactodice*
▲ *H.* (?) *galactodice*
○ *H. microdice*
★ *H. argyrodice*


C
Phulia populations
● P. nymphula


D
Andean Colias
■ C. flaveola
▲ C. blameyi
● C. blameyi tending towards weberbaueri
▼ C. mendozina

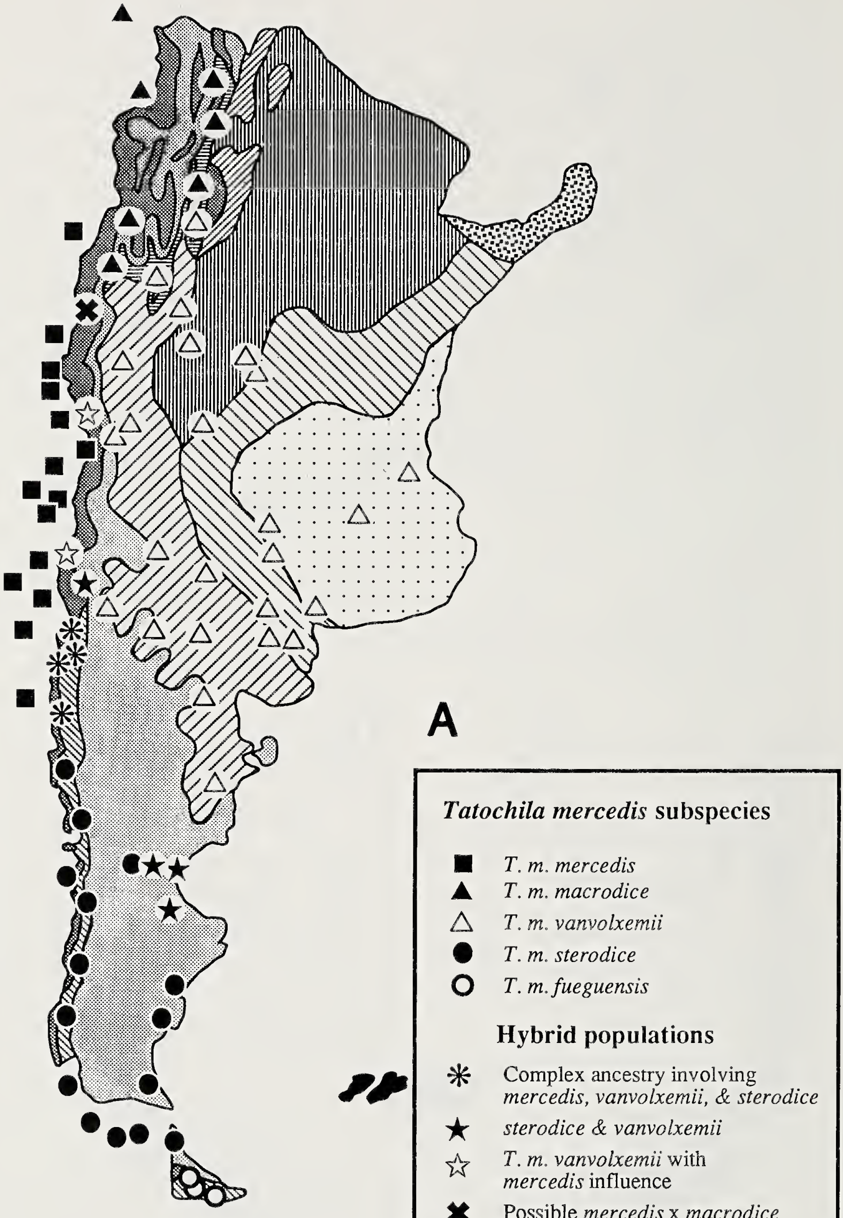
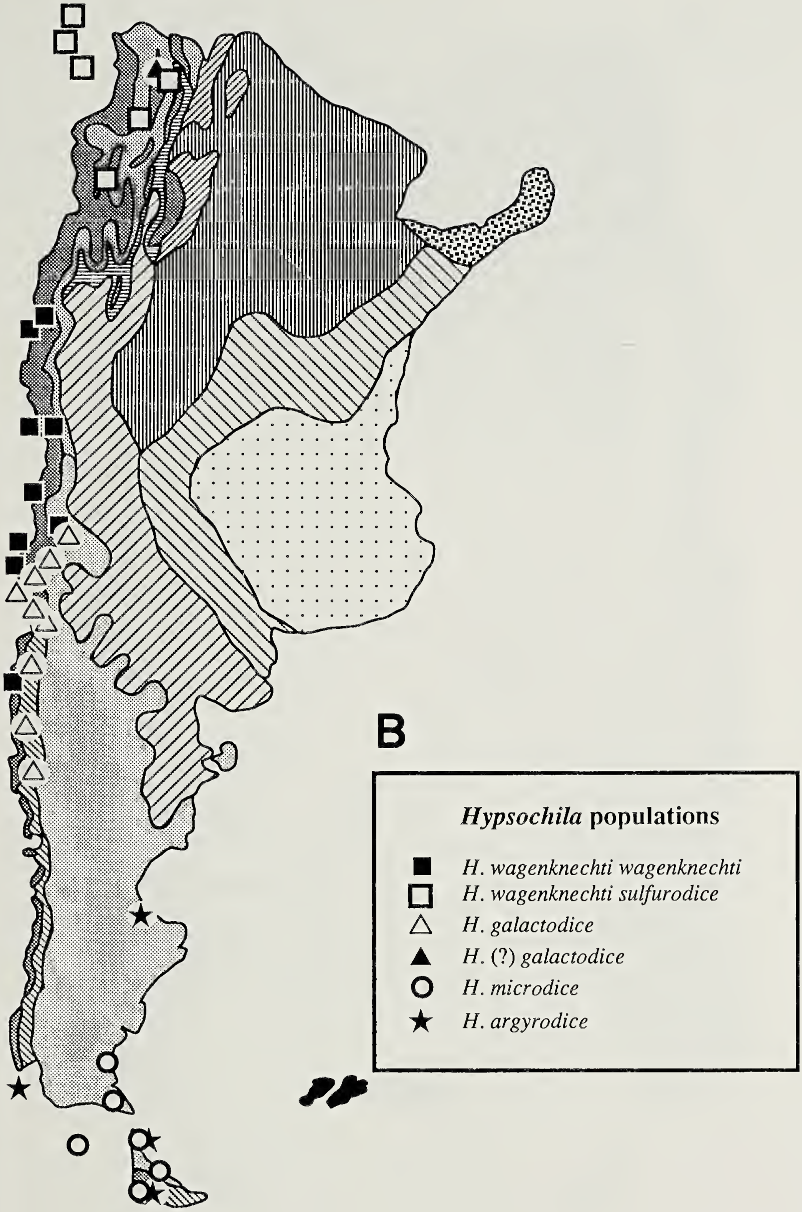
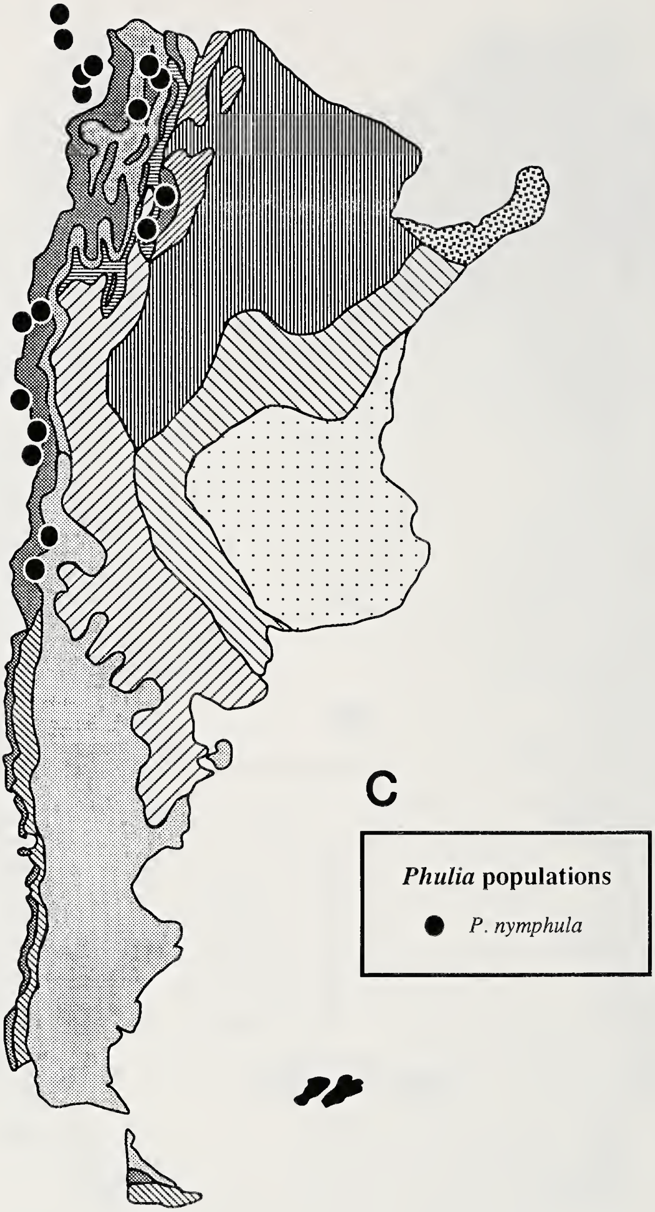
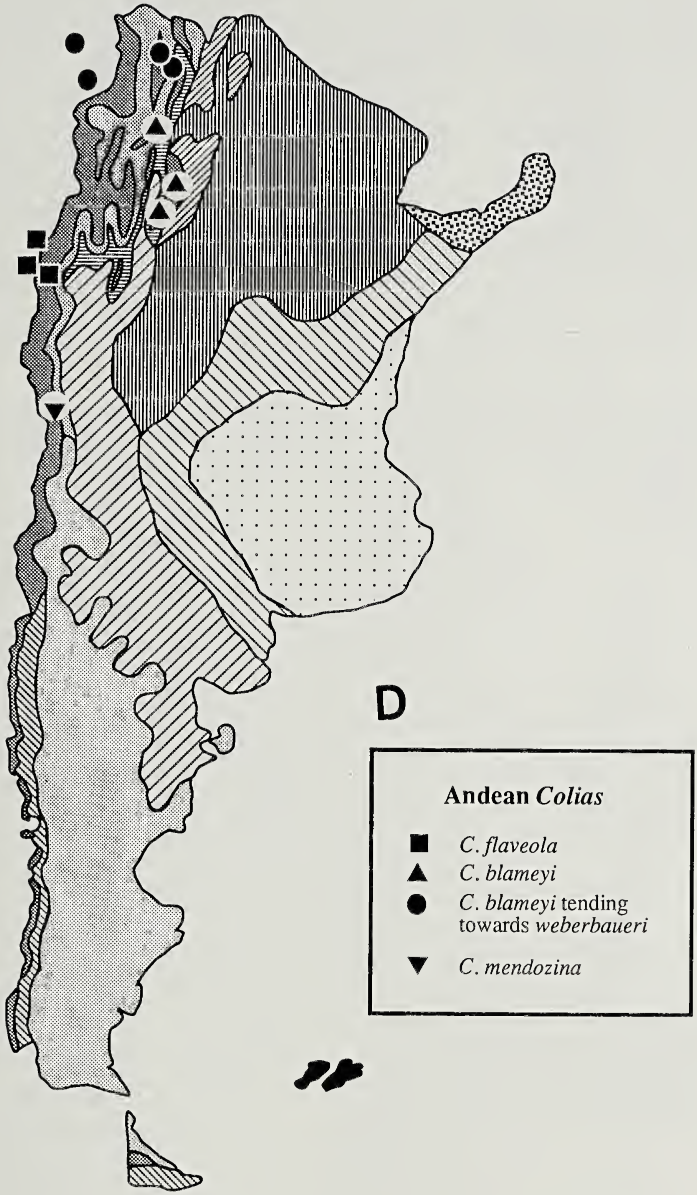

A
Tatochila mercedis subspecies
■ T. m. mercedis
▲ T. m. macrodice
△ T. m. vanvolxemii
● T. m. sterodice
○ T. m. fueguensis
Hybrid populations
✳ Complex ancestry involving mercedis, vanvolxemii, & sterodice
★ sterodice & vanvolxemii
☆ T. m. vanvolxemii with mercedis influence
✖ Possible mercedis x macrodice specimen

Fig. 11A–D. Distributions of selected taxa, superimposed on phytogeography as mapped by Cabrera, 1971 (cf. Fig. 2). A: *Tatochila mercedis* subspecies. B: *Hypsochila*, except *H. penai* and *H. huemul*. C: *Phulia nymphula*. D: Andean *Colias*. Note the absence of *Hypsochila* from the *Sierras Pampeanas*.


B
Hypsochila populations
■ H. wagenknechti wagenknechti
□ H. wagenknechti sulfurodice
△ H. galactodice
▲ H. (?) galactodice
○ H. microdice
★ H. argyrodice


C
Phulia populations
● P. nymphula


D
Andean Colias
■ C. flaveola
▲ C. blameyi
● C. blameyi tending towards weberbaueri
▼ C. mendozina

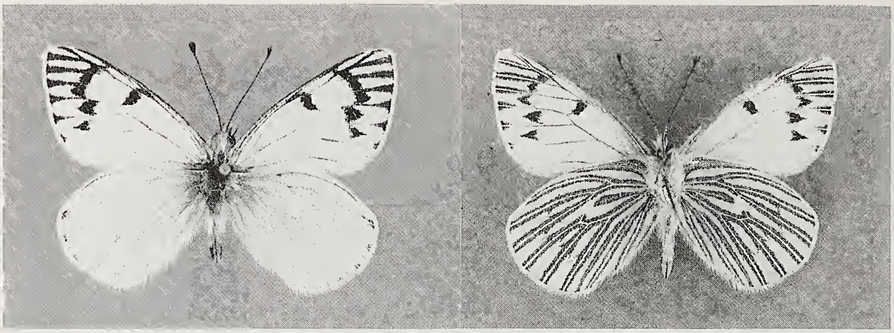


Fig. 12. Unusual male (*mercedis — macrodice* intergrade?) not fitting any named entity in polytypic species *Tatochila mercedis*. Arroyo de Agua Negra, San Juan, 3.XI.1988.

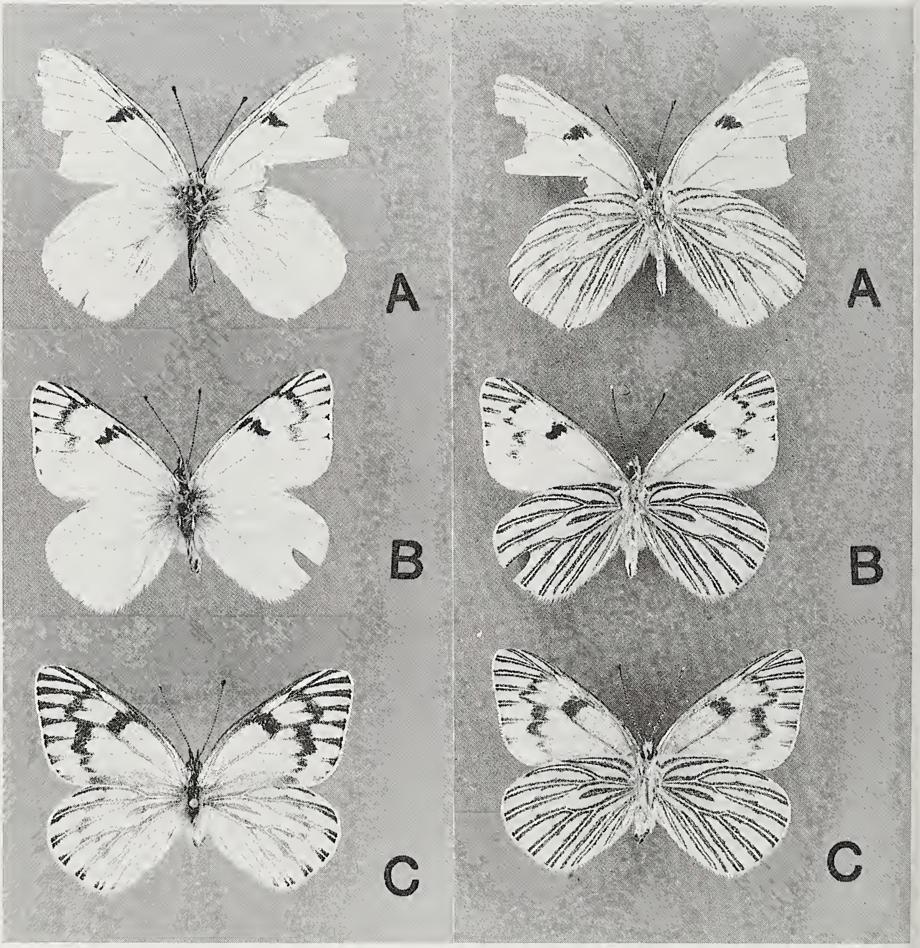


Fig. 13. Wild-collected first-brood males (A, B) and female (C) of *Tatochila mercedis vanvolxemii* from Zapala, Neuquén, 7.XI.1988. Note variable loss of apical FW markings and tendency of these to form a continuous line if present.

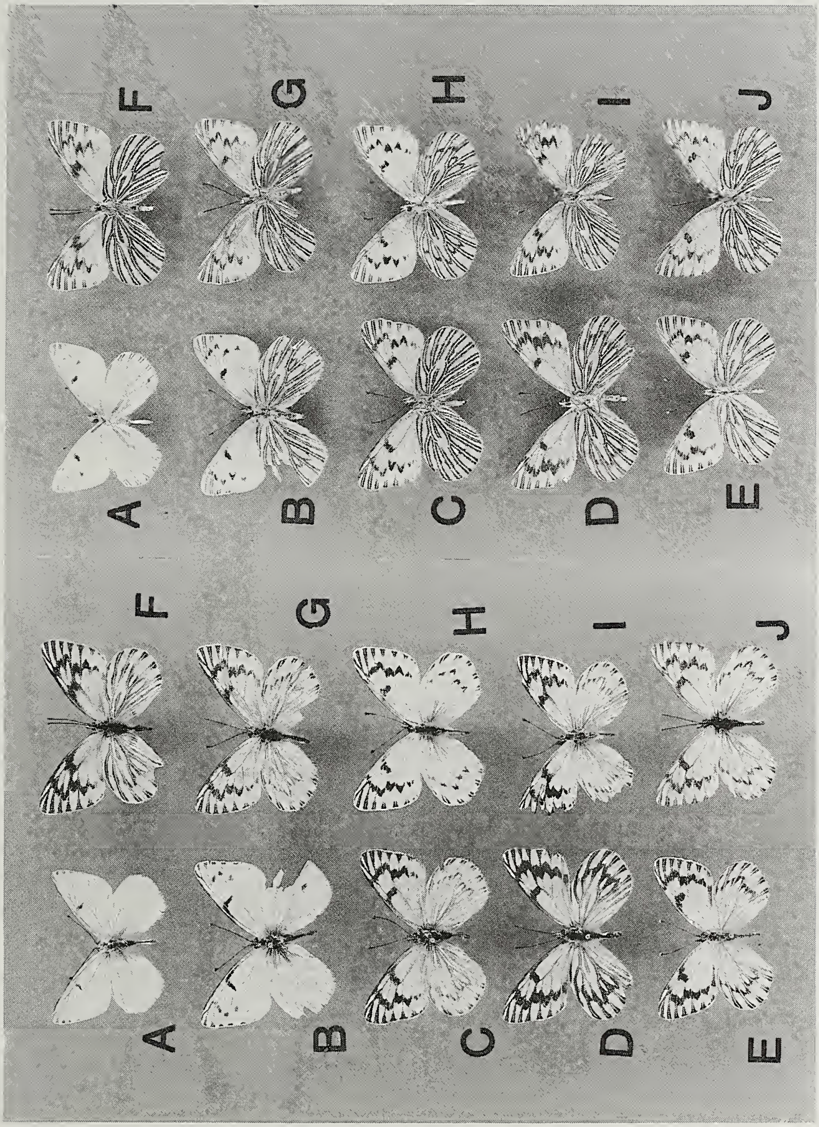


Fig. 14. *Tatochila mercedis vanvolxemii* — *sterodice* intergrades from Loncopué, Neuquén, 8.XI.1988, all collected in the same field. A, B males; remainder females; first brood.

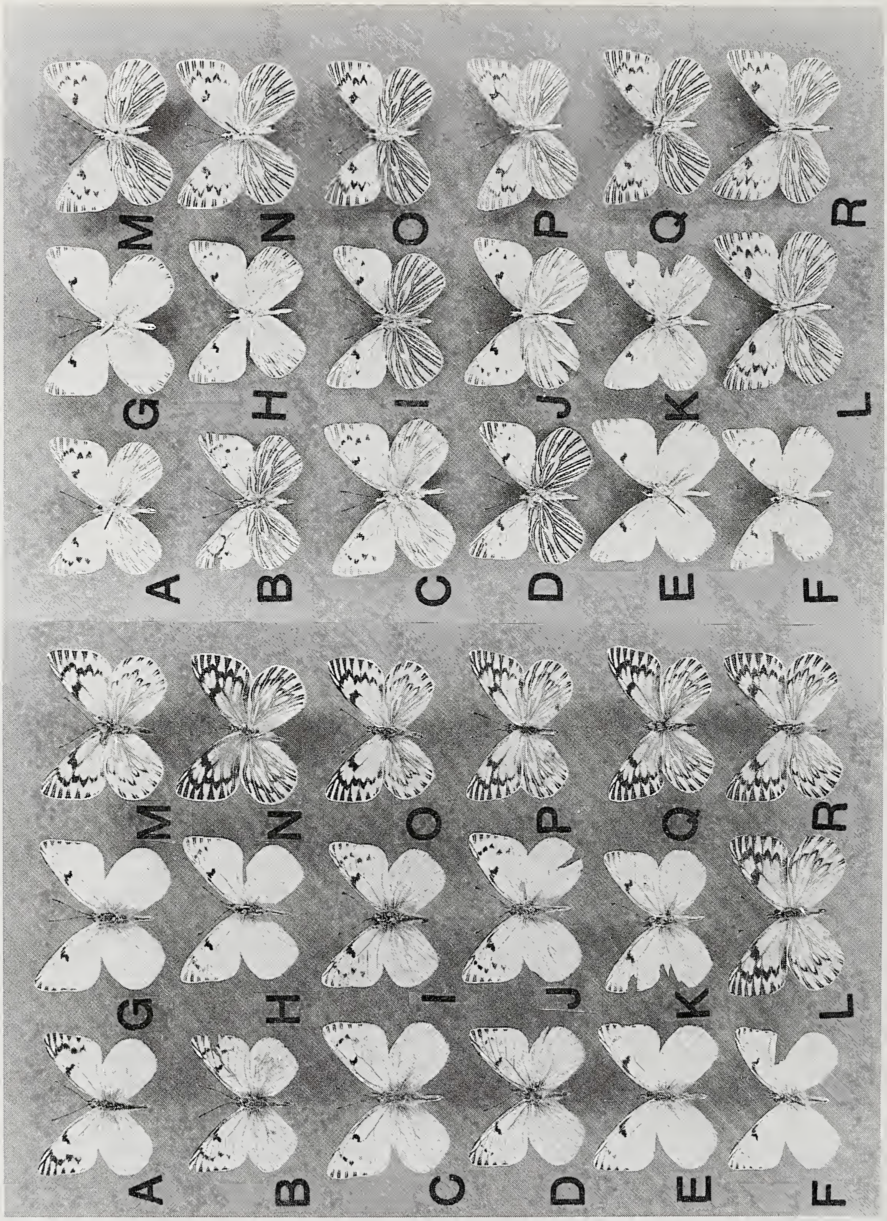


Fig. 15. *Tatochila mercedis vanvolxemii* — *sterodice* intergrades from Barrio Próspero Palazzo, Comodoro Rivadavia, Chubut, 19.XI.1988, all collected in close proximity. A–K, males; L–R, females. Most of these phenotypes are outside the range of variation of "pure" *vanvolxemii*; note tendency of apical FW markings in males to form discrete dots. First brood.

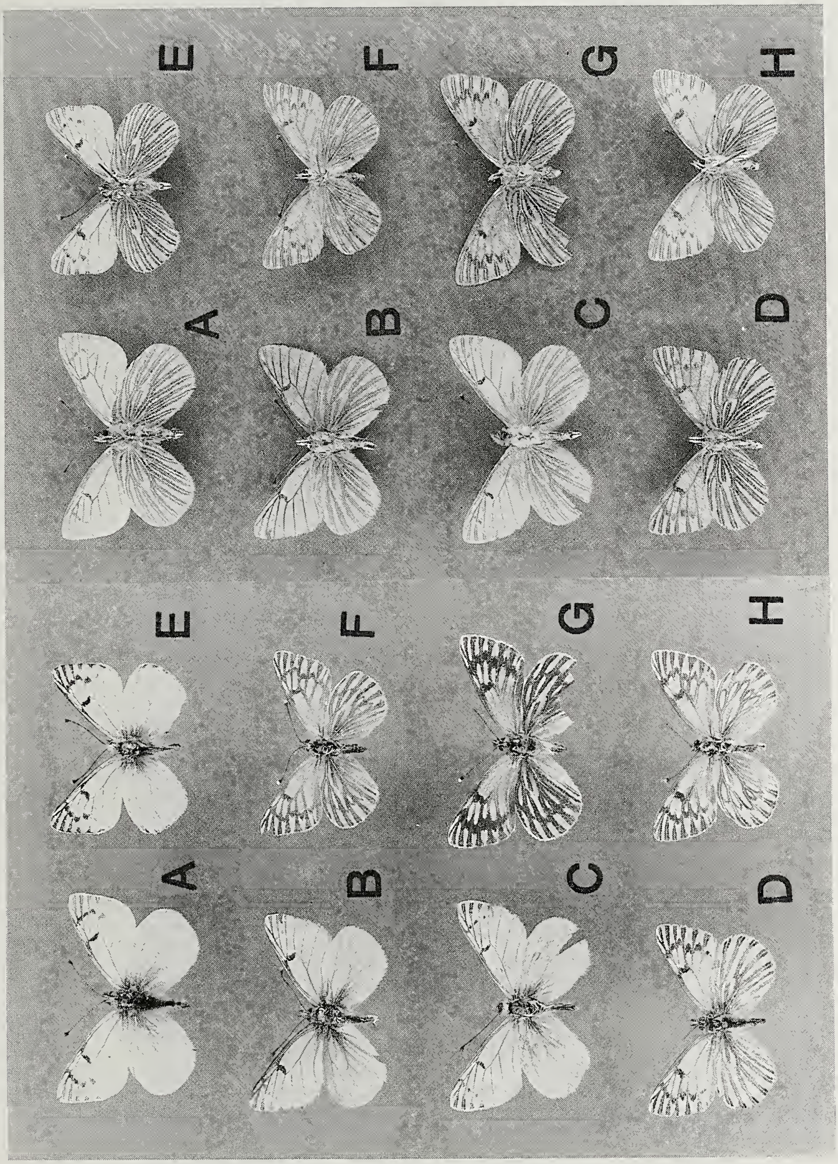


Fig. 16. Intergradation of *Tatochila mercedis sterodice* and *T. m. fueguensis*. A, B, C, E, males; D, F, G, H females. A, Lago Fagnano, Tierra del Fuego, 19.I.1979 (DE) (intermediate). E, Cte. Luis Piedrabuena, Santa Cruz, 20.XI.1988 (*sterodice*). All others from La Esperanza, Santa Cruz, 130 km NW Río Gallegos, 15.I.1979 (DE) (complete intergradation).

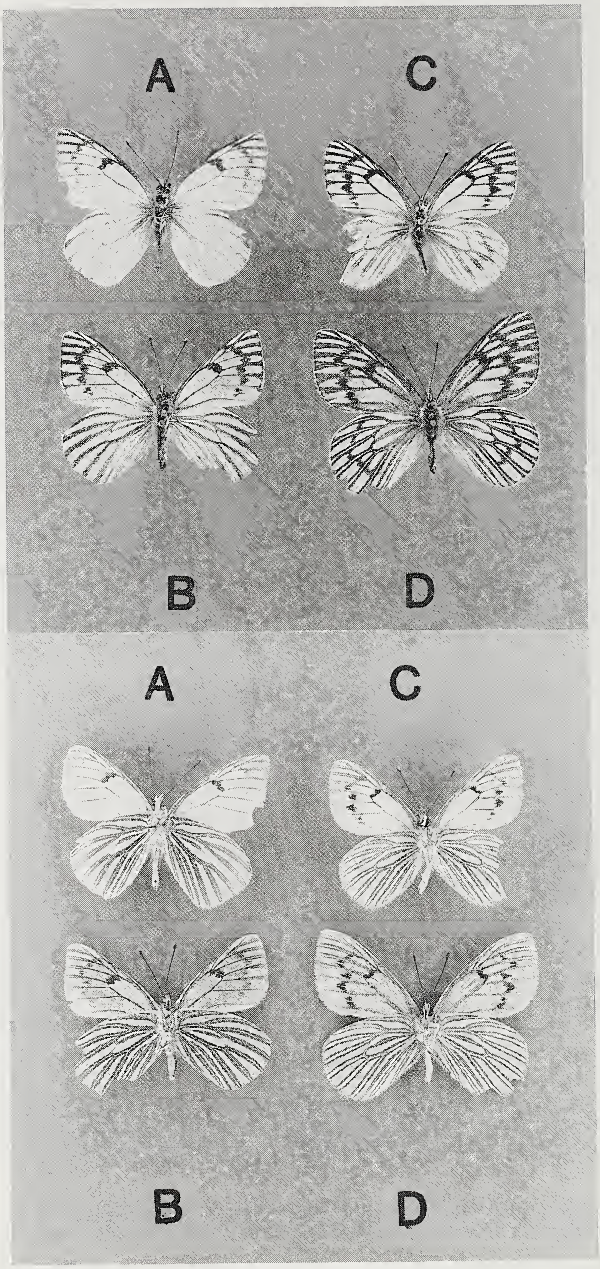


Fig. 17. High-altitude *Tatochila* from NW Argentina. A, *T. inversa* male, Cerro Amarillo, Jujuy, 4.I.1980 (RE). B, *T. inversa* female, Cerro Zapallar, Salta, 22.I.1986. C, *T. distincta distincta* male, Abra Infiernillo, Tucumán, 20.I.1986. D, *T. distincta*, female, Cerro Zapallar, Salta, 22.I.1986. The male *inversa* is the first figured from Argentina.

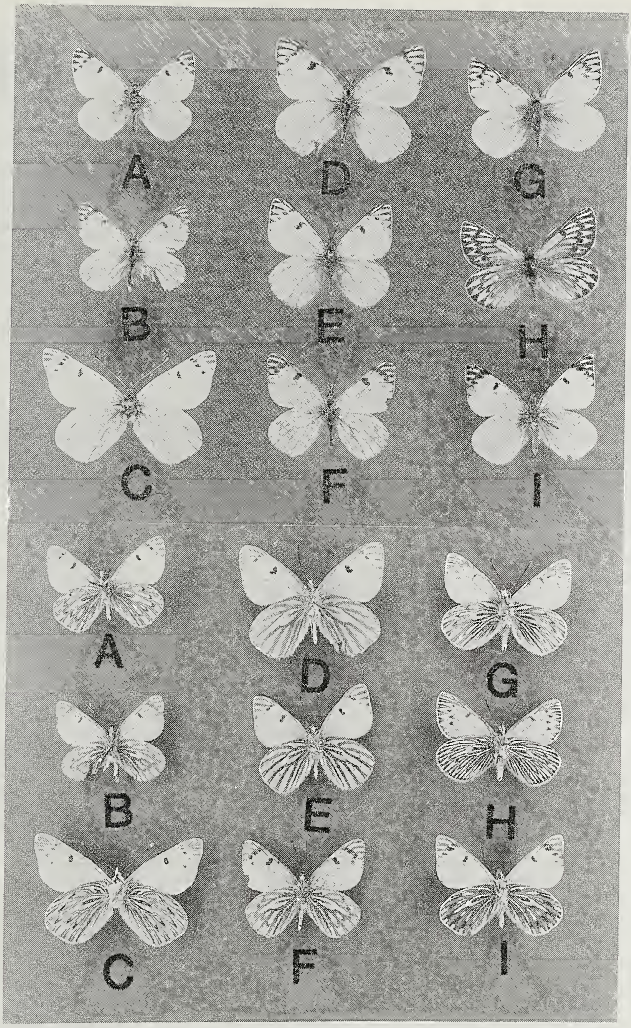


Fig. 18. Various *Hypsochila*. All males except H, female. A, *H. wagenknechti sulfurodice*, Chile, Mamiña, Tarapacá, 30.IX.1974 (J. Herrera). B, same, Tres Cruces, Jujuy, 7.II.1984. C, *H. argyrodice*, Fitz Roy, Santa Cruz, 11.II.1979 (DE). D, E, F all Cerro Amarillo, Jujuy, 4.I.1980 (RE): D and E resemble *H. galactodice*, F resembles *H. w. sulfurodice*. G, H, *H. microdice*, Río Grande, Tierra del Fuego, 25.XI.1988. I, *H. w. wagenknechti*, aberration, Arroyo de Agua Negra, San Juan, 3.XI.1988 (first brood).

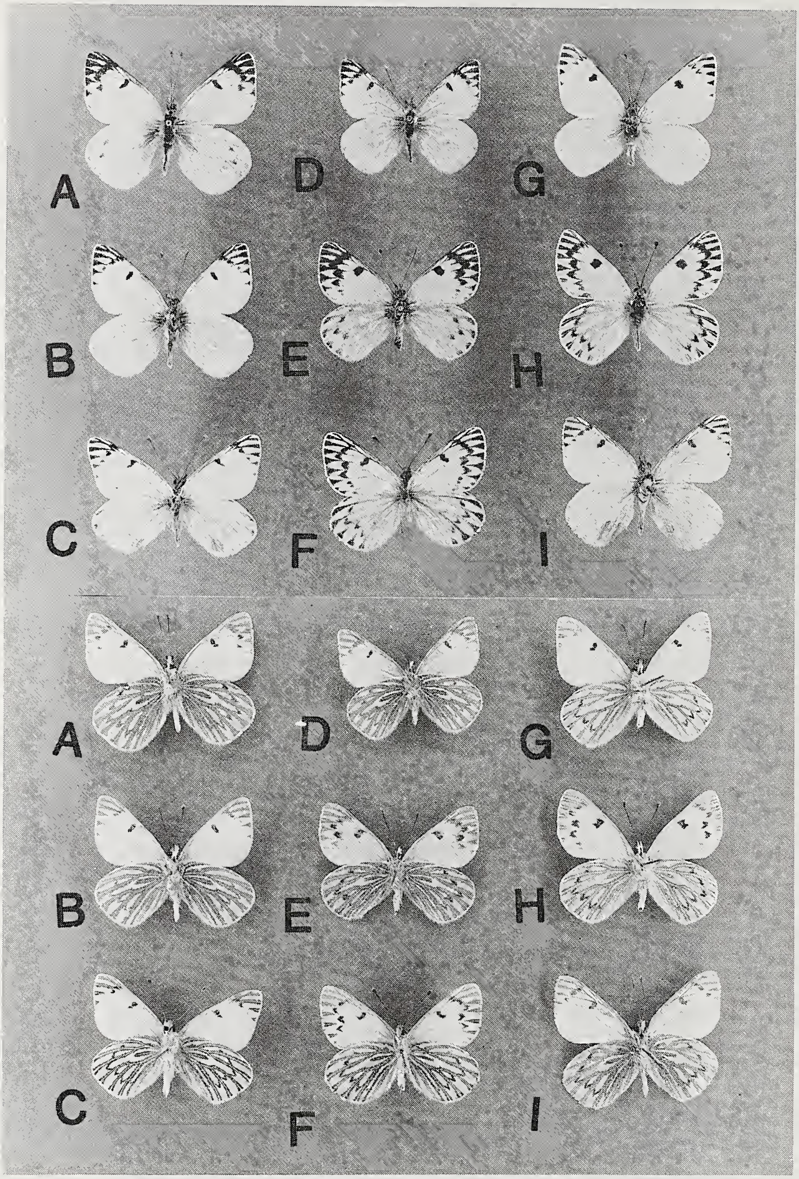


Fig. 19. Various *Hypsochila*. A, B, C, D, G, I males; E, F, H females. A, *H. w. wagenknechti*, Chile, Los Libertadores, Prov. Los Andes, 27–28.I.1983 (second brood). B, E, same, Arroyo de Agua Negra, San Juan, 3.XI.1988 (first brood). C, F, *H. galactodice*, Esquel, Chubut, 17.XI.1988 (first brood). D, *H. w. wagenknechti*, Chile, La Parva, Prov. Santiago, 24.XI.1982 (first brood). G, H, *H. galactodice*, bred without diapause ex Esquel, Chubut, emerged 23–25. XII.1988. I, Species uncertain (*wagenknechti*? *galactodice*?), Cordón del Viento, Neuquén, 28.I.1985.

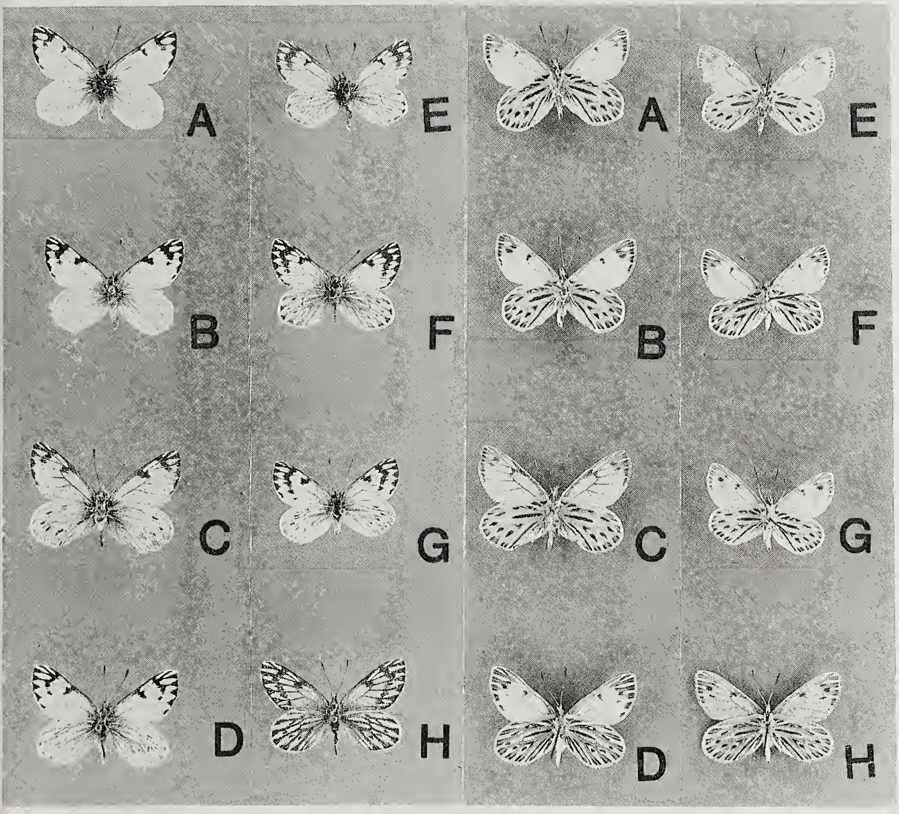


Fig. 20. *Phulia nymphula*. A–D, males; E–H, females. A, B, E, F, G, all Paso Bermejo, Mendoza, 31.X–1.XI.1988 (1st brood; G is a white, male-like female, E is phenotypically similar to *Pierphulia* above). C, Cordón del Viento, Neuquén, 28.I.1985. D, H, Esquinas Blancas, Jujuy, 7.II.1984. D and H are quite typical of *puna* specimens, with longer wings, heavier female pattern, and a more straw, less pinkish color below.

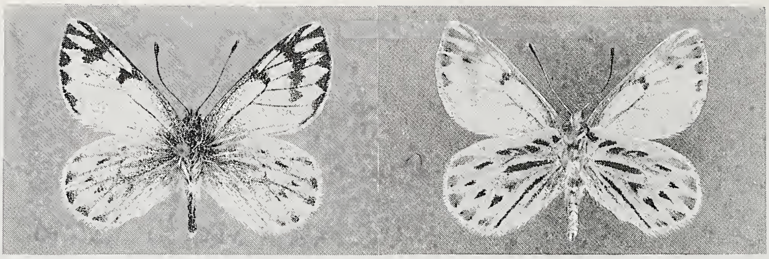


Fig. 21. Mosaic gynandromorph *Phulia nymphula* from Paso Bermejo, Mendoza, 31.X–1.XI.1988. The left FW is apparently all male, the right FW all female, both HW mostly female (left 7/8, right 2/3); the external genitalia are malformed and intermediate. This is the first gynandromorph reported in nature for any Andean pierine.

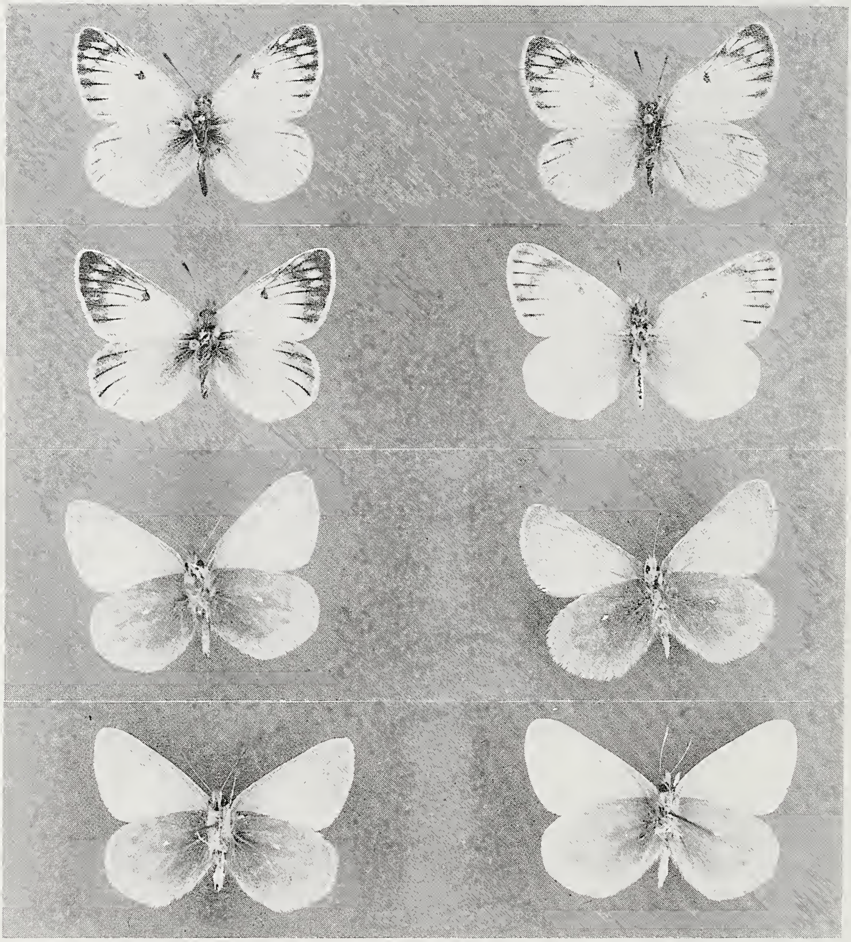


Fig. 22. *Colias flaveola* from Arroyo de Agua Negra, San Juan, 3.XI.1988, males at left in both views.

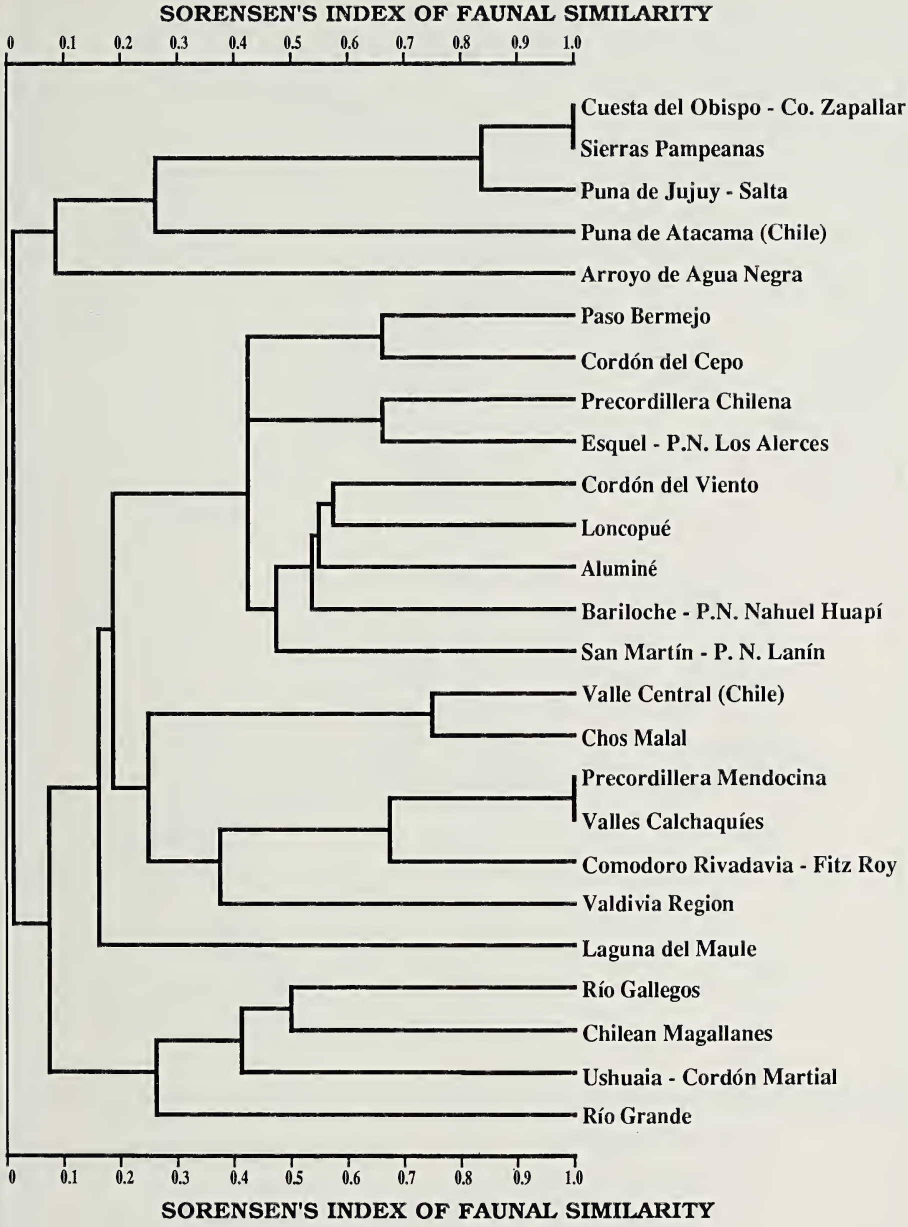


Fig. 23. Dendrogram generated by cluster analysis (UPGMAA) showing relationships among selected faunas compared in Tables 1–3. (For purposes of calculation, species and subspecies were treated equally.)

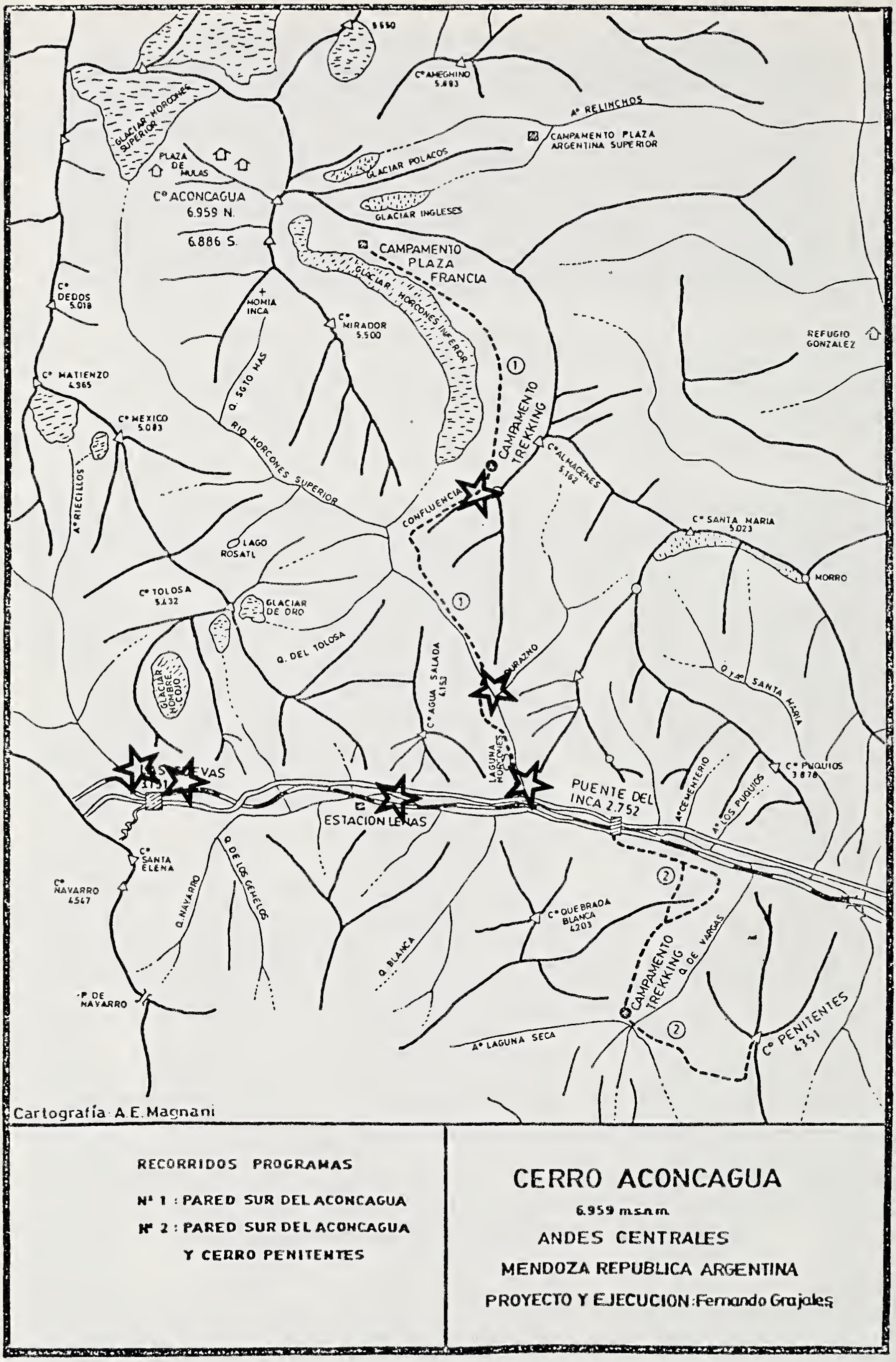


Fig. 24. Argentine sketch map of the Parque Provincial Aconcagua, Mendoza, showing (stars) locations of known suitable *vegas* for the occurrence of *Colias mendozina*. Actual captures are from Quebrada de los Horcones, just NW of Puente del Inca near the middle of the map.